MORPHOLOGICAL AND PHYSIOLOGICAL RESPONSES OF
DWARF ELEPHANTGRASS [Pennisetum purpureum (L.) Schum.]
TO GRAZING MANAGEMENT

BY

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OF THE UNIVERSITY OF FLORIDA IN
PARTIAL FULFILLMENT OF THE REQUIREMENTS
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Dedicated to my parents,

Braulio and Zélia,

my wife Teresinha,

my daughters,

Juliana and Alice,

and to Armando

and Cecília

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Morphological and physiological characteristics of dwarf
elephantgrass [Pennisetum purpureum (L.) Schum.] were studied in a
grazing trial conducted in 1982 at the University of Florida,
Gainesville.

The grass was subjected to the effects of two management factors,
each at five levels as follows: length of grazing cycle (GC)
(continuous grazing, 14, 28, 42, and 56 days) and grazing pressure
(GP) (500, 1000, 1500, 2000, and 2500 kg of leaf dry matter ha^{-1} left
after grazing). A grazing cycle consisted of a 2-day grazing period
followed by an appropriate rest period to attain the desired length of
GC. Response surface methodology was used to study 13 treatment
combinations, each with 2 replications, arranged in a modified non-
rotatable central composite design. The data obtained were analysed
using a complete second order polynomial model.

Increases in GC and decreases in GP increased plant height,
apical meristems height, stem height, number of internodes per tiller,

DM produced by live and dead leaves, DM production of leaf blades (LB), leaf sheaths (LS), and stems (S), area of green LB, and number of dead leaves per main tiller. The percentage of apical meristems eliminated was greater under continuous grazing and high GP. The number of axillary buds per tiller was depressed under high GP. Shorter internodes were observed at short GC and high GP. Leaves per main tiller increased when GP was decreased.

Main tillers per plant and basal tillers per tiller increased with decreased GC and increased GP. Primary tillers constituted the predominant form of tillering in this grass.

Grass LB/(LS + S) ratio was greater at long GCs in combination with low and high GPs.

Concentrations of TNC in stem bases of the grass were affected mainly by the length of GC and were lower at short GCs and high GPs.

The results obtained in this experiment indicate that dwarf elephantgrass has the ability to adapt itself to different grazing situations and should be considered as a promising species for pastures.

INTRODUCTION

Increasing food scarcity in many areas of the world is cause for great concern. Shortage of high-quality protein and particularly meat protein, is the most striking problem. There is an urgent need for substantial intensification of grassland and animal production as the world population continues to grow at a fast rate.

Grazinglands provide a major portion of the feed requirement of livestock for the production of meat, milk, wool, and other animal products. Legumes and various herbaceous species contribute to overall available feedstuff, but in most pastures, grasses predominate. Of 10,000 species of Gramineae only about 40 are actually cultivated as pastures based on their potential for forage (Crowder, 1981; Crowder and Chheda, 1982).

As grasslands developed, natural selection of adapted grasses occurred. Many adaptive traits may have enabled them to withstand grazing. Usually, a plant's reaction to grazing involves more than one mechanism of adaptation and these may be ecological, morphological, or physiological (Hodgkinson and Williams, 1983). In the last 30 years much research has been done to explore these adaptation mechanisms in an endeavor to find superior genotypes for use in particular environments. As a result, several new varieties created by the work of man, have assumed considerable economic importance.

Elephantgrass [Pennisetum purpureum (L.) Schum.] is valued for its high herbage yields, competitive vigor, persistence, palatability, and good quality herbage (Bogdan, 1977). Although widely cultivated as a fodder plant, it is not commonly used in pastures. Many researchers have suggested that the main limitation of elephantgrass under grazing results from management problems deriving from its growth habit. Recently, the discovery in the elephantgrass populations of genotypes with dwarf characteristics has inspired renewed interest in the use of this species for pastures.

After extensive research, it is now well recognized that the regrowth of tropical grasses is influenced by both the plant's morphological and physiological conditions at time of defoliation as well as by other factors like climate, soil, nutrients, and light. The basic morphology and physiology of tropical grasses, however, have not been studied under grazing.

Dwarf elephantgrass appears to be a promising forage for pastures in the tropics and subtropics. In order to insure its persistence and productivity in the pasture, the regrowth mechanisms of the species should be studied.

In this research, an adaptation of response surface methodology to grazing trials (Mott, 1982) was used to analyze the effects of grazing pressure and length óf grazing cycle on morphological and physiological components of regrowth of a dwarf elephantgrass pasture. The main objective was to study, under grazing conditions, the responses of the plants to different systems of grazing management.

LITERATURE REVIEW

Pennisetum purpureum: Origin, Distribution and
Morphological Characteristics

Pennisetum purpureum (L.) Schum. is a robust perennial which
occurs naturally throughout tropical Africa. Taxonomically it belongs
to the tribe Paniceae of the subfamily Panicoideae of Gramineae. It
is commonly called elephantgrass or napiergrass, and by many other
names usually given to different varieties. The grass produces little
or no seed and is normally propagated by stem cuttings. Due to its
high herbage yields, competitive vigor, persistence, palatability, and
good quality herbage it has been introduced into practically all
tropical countries (Bogdan, 1977).

Because of its tolerance to low temperatures, it has spread far
beyond the tropics. Introduced into the United States from Rhodesia
in 1913 (Thompson, 1919), it furnishes herbage for grazing from May to
November in north central Florida (Blaser et al., 1955). Top growth
can be killed by light frosts but roots and rhizomes will endure low
temperatures, unless the soil is frozen (Bogdan, 1977).

There are many morphological differences among cultivars of
elephantgrass. The height of plants, the length of internodes, the
hairiness of stem nodes and leaf sheaths, the size of leaves, the
thickness of stems, the size of tufts, the number of tillers per
plant, and general vigor may vary (Bogdan, 1977). There are also
differences in size, color, and density of panicles as well as in the
number of chromosomes (Bogdan, 1977; Muldoon and Pearson, 1979c).

In general, elephantgrass is a perennial which combines an erect
growth habit with rhizome development. It forms large broad clumps
containing numerous cane-like stems. The stems have numerous nodes
and internodes. Leaves are glabrous or hairy, varying in length from
30 to 120 cm, and width from 1 to 5 cm. This grass often produces 50
tillers per plant and depending on environmental constraints it grows
to a height of 2 to 4 m (Grof, 1959; Bogdan, 1977).

Genetic improvement has been attempted by crossing P. purpureum
with other species within the same genus, e.g., P. americanum, as well
as by intraspecific crosses. The hybrid Pennisetum is an erect bunch
grass and resembles elephantgrass in gross morphology (Muldoon and
Pearson, 1977).

Recently, a dwarf strain of elephantgrass, known as line N-75,
was isolated from a population of P. purpureum in the Coastal Plains
Experimental Station, Tifton, Georgia. In 1979 this material was
introduced at the Beef Research Unit of the University of Florida
where it has been studied (Boddorff, 1982; Castillo-Gallegos, 1983;
Veiga, 1983).

Plant Introduction and Desirable Characteristics in Pasture Plants

The relationship between plant and grazing animal is mutually
interactive because the animal influences the behavior of the plant,
which in turn influences the animal (McNaughton et al., 1982). The
grazing tolerance of many grasses is dependent upon a combination of
adaptive mechanisms resulting from a long and intimate coevolution
between grasses and large grazing ungulates (Baker, 1978; McNaughton

et al., 1982). This interactive evolution generated genetic variability and a wide diversity of species and ecotypes available today. It is this diversity that will permit the most efficient and rapid improvement of pasture lands in vast areas of the world (Luse, 1979).

The need to preserve the forage germplasm upon which man relies to feed his animals and hence, indirectly, himself has been emphasized. The strategies of the collection and improvement of tropical forages were recently discussed by Mott and Hutton (1979). They suggested that all available scientific technology should be applied to the rapid development of new forage cultivars, which will improve the quantity and quality of forage production. The following charactersitics are thought of as basic requirements of an introduced species: high yield of dry matter, good quality forage, capacity to associate with other desirable species and ease of propagation and establishment. Other desirable features include: seedling vigor, high growth rate, tolerance to drought, cold, heat, and grazing, resistance to disease and insect attacks, seed production, and competitive ability (Williams et al., 1976; Humphreys, 1978; Whiteman, 1980). The importance of such factors depends upon the characteristics of the region and the production system to be used. In Australia, a general growth index was suggested by Fitzpatrick and Nix (1970) to compare different environments and their effect on the growth of pasture species. Climatic zones applicable to tropical species are presented by Reid (1973) and zoning of forage species has been suggested in São Paulo, Brazil (Jones, 1974). In any case high performance in

different environments and adaptation to a wide range of local
management conditions is of the greatest importance (Humphreys, 1978;
1981).

Forage Evaluation and the Development of Grazing Systems

It is well accepted that forage plants should be carefully
managed to optimize yield, quality and persistence.

In grazing systems one must compromise some yield potential to
get enhanced quality and vice-versa. According to Dahl and Hyder
(1977) the skill comes in choosing how far to go in maintaining high
quality before the recovery potential of the species is irreversibly
penalized. The conflict between increasing production or quality of
forage and the stability of the pasture is of particular importance.
In this context, persistence of the species must be considered as the
most valuable attribute of an established pasture. This is stressed
because the cost of establishing new pastures can affect the economic
viability of any project.

Approaches to be followed in testing forage plants were
established by Mott and Moore (1970) with the definition of a forage
evaluation scheme in five stages. Screening of breeders lines and
introductions, small plot clipping studies, and evaluation of the
environmental adaptation of the species are performed in stages I and
II. In stage III the use of animals is required to test the response
of plants under grazing conditions. Output per animal is determined
in stage IV and in the final stage, practical feeding systems are
developed. Interesting to notice in this scheme is the determination

of _in vitro_ dry matter digestibility (IVDMD) in stages I through IV.
This allows the elimination of an undesirable species at an early
stage of evaluation (stages I and II) and gives a good indication of
the quality of the forage being grazed (stages III and IV).
Furthermore, a large spectrum of disciplines should be involved in the
development of new cultivars. The agronomist, the animal
nutritionist, the forage physiologist, the plant breeder, and the soil
fertility specialist, working together, will have a greater chance of
success when releasing a new cultivar.

It has been indicated, in the selection process of new cultivars,
that persistence under grazing or cutting becomes very important and
perhaps more important than yield potential (Mott and Hutton, 1979).
So far, this suggests that the use of grazing animals at an earlier
phase in the process of evaluation would save time and money.

An extensive plan, consisting of protocols A and B, has been
presented by Mochrie et al. (1981) to evaluate new forages. Protocol
A has six phases: Phase I) collection of material and conception of
its potential. IVDMD are performed here and in subsequent phases;
Phase II) persistence and animal preference; Phase III) detailed
management and qualitative animal response; Phase IV) seed increase or
expanded vegetative source and quantitative animal evaluation; Phase
V) release and on-farm implementation and observation of response to
herd or flock utilization; Phase VI) refinement and continued
improvement. Protocol B was developed to evaluate a modified cultivar
of an established variety and comprises four phases: Phase I)
productivity and quality (IVDMD); Phase II) persistence and animal

preference; Phase III) management and qualitative animal response; Phase IV) seed increase or expanded vegetative source and quantitative animal response. Although theoretical, the scheme of Mochrie et al. (1981) is highly desirable in recognizing the early use of grazing animals in the process of forage evaluation.

A new approach in forage germplasm evaluation, comprising three steps, has been recently proposed by Mott (1982). He emphasized that the grazing animal should be brought into the evaluation scheme as early as possible because the stress imposed on the plant by the animal can affect persistence and production of the pasture. In the first step, during the first year after planting, only agronomic characteristics are recorded. In the second year, ten or less introductions are subjected to different systems of defoliation to identify differences in acceptability and responses to defoliation. One to three superior lines are selected in step two and their response to the components of the grazing management and other variables appropriate to regional systems of production are evaluated in step three.

Mott (1982) suggested that more complex statistical designs, such as the central composite, can be used in order to provide information on a wide combination of circumstances involved in the interactions between forage plants and the grazing animal.

Some understanding of the likely reaction of new introductions to management could be required before their inclusion in animal production tests (Morley, 1978). In many cases, information on measurements which do not involve animals and measurements of plant

responses to grazing may allow the discarding of the species without
further tests.

Although the final choice of pasture species should rely on
animal production, many plant attributes can be important if not
critical (Whiteman, 1980; Wheeler, 1981). Because measurements of
animal production involve substantially more resources than are needed
for measurements of vegetation alone, forage evaluation has been
limited to the effects of animals on plants with supplementary
information on digestibility, diet selection and intake (Morley,
1978).

The development and improvement of a grazing system depends on
the plant-animal relationships which are pertinent to that system and
therefore a compromise may be needed to achieve the best use of
available resources.

Forage Quality

In many forage-livestock systems, quantity and quality of the
feed ingested determine animal performance (Moore, 1980a). The amount
of forage available to each animal is the result of management
decisions such as choice of grasses and legumes, pasture maintenance
with fertilizers and weed control, choice of grazing system, selection
of livestock and use of supplementary feeding (Crowder and Chheda,
1982). Animal performance or output of the grazing animal provides
the best estimate of the quality of the available forage (Mott, 1959).
Indeed, low production per animal on tropical pastures has been
associated with low forage quality in terms of voluntary intake and

digestibility (Moore and Mott, 1973). The interaction of chemical and physical characteristics of the forage with mechanisms of digestion, metabolism, and control of voluntary intake determine the level of digestible energy intake and animal performance (Moore, 1980a). When it is not possible to conduct a long-term production trial, alternative definitions of forage quality may be used. These include voluntary intake of digestible energy, total digestible nutrients, digestible dry matter or digestible organic matter (Moore, 1980b).

Pasture swards differ in vertical development and structure of the canopy, bulk density of the herbage, leaf/stem ratio, arrangement of tillers, and accessibility of leaves (Crowder and Chheda, 1982; Hodgson, 1982). When allowed to graze freely, animals select species and plant parts of higher nutritive value (Arnold, 1981; Hodgson, 1982). Therefore, the grazing process affects the sward structure by changing the proportion of leaf, stem, dead material, and the botanical composition of the pasture (Chacon et al., 1978; Whiteman, 1980; Blaser, 1982). Leaf yield increases with time but it is accompanied by a decrease in digestibility (Blaser, 1982). Separation of the vertical components will show that digestibility of leaves and stems differ from the upper to the lower part of the plant (Wilson, 1976; Chacon et al., 1978). In the early stages of growth the herbage consists almost entirely of leaves. As grasses age, stems comprise a greater percentage of the plant. Chacon et al. (1978) found that leaf/stem ratio, especially in the top of the sward, strongly affects animal performance.

It has been suggested that intake and digestibility of forage plants can be genetically improved (Hacker, 1982). So far, there is a general agreement among plant and animal scientists that by introducing leafier varieties an increase in forage quality should prevail. In this context, it should be expected that the introduction of a dwarf gene in populations of Pennisetum purpureum would reduce internode length, plant height, and stem percentage. Hanna et al. (1979) reported that the d_2 dwarf gene in pearl millet (P. americanum) reduces plant height by 50%, and dry matter yields by 9 to 13%, depending on cutting frequency.

The results obtained with dwarf elephantgrass, line N-75 (P. purpureum), under cutting experiments (Boddorff, 1982; Castillo-Gallegos, 1983) and under grazing conditions (Veiga, 1983) indicate that this species has high quality attributes.

Grazing Management

Grazing management involves the manipulation of two biological systems: the pasture sward and the grazing animal. Factors affecting either system will ultimately influence the output per animal (Crowder and Chheda, 1982). The terminology used in grazing management studies has been presented by several authors (Mott, 1960, 1980; Morley, 1978; Hodgson, 1979; Thomas, 1980). Before considering animal effects on a pasture certain terms should be defined. Continuous grazing or set stocking is the practice of allowing unrestricted livestock access to any part of the range throughout a grazing season. Rotational grazing is a regular sequence of grazing and rest from grazing for a specific

area of sward. In this case the animals are moved from one pasture to another on a scheduled basis. Grazing period is the length of time during which a particular paddock is grazed. Rest period is the length of time between the end of one grazing and the start of the next. Grazing cycle is the length of time between the beginning of one grazing and the beginning of the next and therefore includes the grazing period plus rest period. Stocking rate is the number of animals of a specific class per unit area of land over a period of time. Grazing pressure is defined as the number of animals of a specific class per unit weight of available forage (Hodgson, 1979).

When discussing grazing management it is worthwhile to remember that the pasture ecosystem is probably more sensitive to overgrazing and undergrazing than is the animal which is grazing the pasture (Mott, 1980).

Leafe and Parsons (1983) pointed out that there is a conflict between factors needed to maximize animal production and those needed to maximize sward production. Maximum sward production requires the retention of a full canopy of photosynthetically efficient leaves whereas maximum animal production requires the consumption of as much as possible of the young and most nutritious foliage. Under continuous grazing, high rates of net photosynthesis of expanding and recently expanded leaves did not compensate for small leaf area when grazing intensity increased. Deinum et al. (1983) suggested that the good performance of _Lolium perenne_ swards under continuous grazing may be partly due to less death and decay of leaves than with rotational

grazing. However, root production may be smaller under continuous grazing because of the continuous demand for replenishment of leaves.

Results of liveweight gains in continuous and rotational grazing systems were reviewed by Mannetje et al. (1976). Out of twelve trials where comparison was possible, in eight trials continuous grazing was superior, in two trials there were no differences, and in another two trials rotational grazing was superior. Because differences among grazing systems are often not large it has been indicated that the conversion of pasture to animal products relies more on stocking rate than grazing system (Humphreys, 1978; Morley, 1978; Whiteman, 1980). The relationships between stocking rate and animal output have been discussed by several authors (Mott, 1960, 1980; Jones and Sandland, 1974; Morley, 1978). The model proposed by Mott (1960) has probably had the greatest influence on pasture and animal scientists in the tropics. The relationship he proposed for stocking rate and gain per animal indicated that product per animal shows little decrease as stocking rate increases from the undergrazed condition to an optimum rate, whereas product per hectare shows a very rapid rise. Beyond the optimum stocking rate, based on an optimum grazing pressure, a marked decrease occurs in gain per animal. In contrast, other authors have indicated that production per animal declines linearly with increasing stocking rate (Jones and Sandland, 1974).

Responses of Forage Plants to Defoliation

Defoliation has been quantified in terms of frequency, intensity and time. Frequency is considered as the time interval between

successive defoliations. Intensity is measured by the proportion of
the plant parts removed and the characteristics and amount of material
remaining after defoliation. Time or season of defoliation is
considered in relation to the developmental stage of the plant and the
nature of current environmental conditions (Humphreys, 1966, 1981;
Harris, 1978).

The responses of forage plants to defoliation has been discussed
by Milthorpe and Davidson (1966), Humphreys (1966), Jewiss (1966),
Hyder (1972), Youngner (1972), Gomide (1973), Dahl and Hyder (1977),
Harris (1978), Vickery (1981), Deregibus et al. (1982), and Dyer et
al. (1982). All of these authors emphasize in a general way that
regrowth after defoliation may be influenced by the number of sites
from which new growth can take place (i.e., the morphology of the
plant, by the amount of leaf area remaining after cutting or grazing
and by the reserve carbohydrates in the residual tissue). In
addition, morphological and physiological responses of plants are
always associated with environmental factors such as light, water, and
temperature (Alberda, 1966; Cooper and Tainton, 1968; Cooper, 1970;
Wilson, 1973; McWilliam, 1978; Ludlow, 1978; Turner and Begg, 1978;
Humphreys, 1981).

Most of the available information on reaction of tropical grasses
following defoliation comes from cutting experiments but it is well
known that extrapolating from cutting experiments to grazing practice
is rarely safe. Several differences exist between the effects of
cutting and grazing. Cutting with shears provide a uniform intensity
of defoliation and the data are obtained at constant time intervals.

Grazing, however, affects several basic components of regrowth and forage quality because of selective eating habits of the animal, trampling, and return of animal excreta (Watkin and Clements, 1978; Arnold, 1981). Other factors may also affect the growth and survival of plants after defoliation. These include a deeper root system and the ability to produce seed. Grazing animals usually take repeated bites to harvest an individual plant but the frequency and intensity of grazing of any tiller is influenced by many factors, including stocking rate, bulk density, and length of herbage (Arnold, 1981). Even under intensive grazing of mono-specific grass swards a pattern of grazing occurs and individual plants may escape defoliation for a time. Hodgkinson and Williams (1983) pointed out that when a pasture is grazed the surviving plants usually respond by changes in form and function. Assuming a prostrate growth habit by horizontal tillering or altering their physiological characteristics forage plants adapt themselves to the grazing situation and therefore insure their persistence in the pasture. Species differ in their ability to survive treading (Edmond, 1966) but usually stoloniferous or rhizomatous species are able to withstand heavy and close grazing (Hodgkinson and Williams, 1983). Because considerable genetic variation is available within forage species for many physiological and morphological features, these should be considered in improvement of forage plants (Cooper, 1983).

Responses of Tropical Grasses to Temperature

As a group, subtropical and tropical grasses have an optimum and an upper and lower temperature limit for growth 10°C higher than that

of temperate grasses. These species grow extremely slowly, if at all, at temperatures around 10 to 15°C and the upper limit for growth is approximately 40 to 45°C. Their growth rate is maximum in the range 30 to 35°C (Cooper and Tainton, 1968; McWilliam, 1978).

For many temperate grasses, the optimum temperature for growth, as measured by dry matter increase or relative growth rate, lies between 20 to 25°C (Cooper and Tainton, 1968; McWilliam, 1978). Some growth is possible at temperatures down to 5°C and at the upper extreme most species cease growth in the range from 30 to 35°C.

In response to temperature, pasture plants may vary their growth rate and morphology at any particular stage of development. They alter assimilation rate as a direct consequence of temperature or through the balance between photosynthesis and respiration, and utilize temperature change for the initiation and control of germination and reproduction (McWilliam, 1978).

Ivory and Whiteman (1978a) studied the effect of temperature on growth of buffelgrass (Cenchrus ciliaris), Rhodesgrass (Chloris gayana), green panic (Panicum maximum var. trichoglume), makarikarigrass (Panicum coloratum var. makarikariensis), and kikuyugrass (Pennisetum clandestinum) in two experiments in controlled environments having all possible day/night temperature combinations of (1) 10, 20, 30, and 40°C and (2) 15, 25, 30, and 35°C. They observed that day and night temperature do not act independently but interact in their effects on the growth of these species. The optimum day temperature for maximum growth varies with the associated night temperature, and vice versa. Where day or night temperature were

reduced below optimum values, the respective night or day temperature that maximize growth were reduced. Growth was greatly reduced by constant temperatures of 10 and 15°C, while maximum growth rates occurred at 29 to 35°C day temperatures with 26 to 30°C night temperatures. The effect of temperature on relative growth rate was mediated through its effect on net assimilation rate. Night temperature was found to affect relative growth rate and net assimilation rate independently of day temperature.

Day temperature had a greater influence on tillering than night temperature, but there were distinct species differences; buffel, Rhodes, and makarikari grasses were not significantly affected by day or night temperature, except at 10°C, while green panic and kikuyu grasses were very responsive to change in day and night temperatures. The optimum temperatures for leaf growth and leaf area development in buffel and Rhodes were higher than the optimum temperatures for growth of the whole plant, while optimum temperatures for stem growth were lower. In green panic, makarikari and kikuyu grasses optimum temperatures for all growth components were similar. One important component of leaf growth which affects leaf area is the specific leaf weight (Sw). The mean trend for Sw was to decrease with increasing night temperature but to increase up to a maximum at 31°C with increasing day temperature.

Regrowth yields of elephantgrass (Pennisetum purpureum) were found to be linearly and positively correlated with tiller density, both in the parent crop at harvest and in the regrowth crop, and with average temperature during regrowth (Ferraris and Sinclair, 1980a, 1980b).

Many pasture plants of tropical origin are unable to grow and may show specific damage symptoms at temperatures in the range of 0 to 15°C (McWilliam, 1978).

Estimated critical mean daily temperatures causing cessation of growth in buffel, green panic, and makarikari grasses were about 12°C and for Rhodesgrass and kikuyugrass were about 8°C (Ivory and Whiteman, 1978b). However, with a day temperature of 20°C, critical night temperatures of all species were below 4°C. Where the night temperature was decreased from 14 to 4°C, significant decreases in net assimilation rate but not leaf area ratio occurred after 5 days in Cenchrus ciliaris and Panicum maximum. Over a period of 10 consecutive exposures to a night temperature of 4°C there was a significant decrease in relative growth rate. Leaf stomatal resistance in these same species, however, was decreased in sucessive photoperiods (at 23°C) following continued exposure to 4°C at night.

Rowley et al. (1975) and Rowley (1976) have shown that the more cold tolerant C_4 grasses (such as Paspalum dilatatum, Eragrostis curvula and Cenchrus ciliaris) have the ability to harden, which reduces damage following exposure to frost.

Short-term exposures to low night temperature have been shown to affect subsequent rates of photosynthesis in tropical grasses (West, 1970; Ludlow and Wilson, 1971; Pasternak and Wilson, 1972), although Smith and Pettiford (1970) suggested that in Chloris species and Digitaria decumbens, after an initial large decrease in growth rate following exposure to low night temperatures, a subsequent gradual adaptation led to increased growth rates. Pasternak and Wilson (1972)

showed that reduced photosynthesis could be related to increased stomatal resistance, while West (1970) found change in chloroplast structure.

Three genotypes of _Pennisetum_ growing at day/night temperatures that ranged from 18/13 to 33/28°C were studied by Pearson and Derrick (1977). They reported that leaves at low temperature had low photosynthetic rates, exported ^{14}C more slowly, retained a higher proportion of photosynthate, had higher sucrose concentrations, and aged physiologically more slowly than did leaves growing at higher temperatures.

The optimum temperature for photosynthesis increases with an increase in either CO_2 concentration or irradiance, which suggests that temperature operates primarily through its effect on the biochemical reactions involved in carbon fixation (McWilliam, 1978).

Under high irradiance and ambient CO_2 concentration, net photosynthesis has a broad temperature optimum, similar in most aspects to the optimum temperature for growth of shoots in both temperate and tropical grasses (McWilliam, 1978). This optimum is usually about 20 to 25°C for temperatue species and 30 to 35°C for tropical species (Cooper and Tainton, 1968) and although rates of photosynthesis at this temperature are faster than many temperate species at their optimum, the C_4 grasses are at a relative disadvantage at temperatures below 15°C (Cooper, 1970), possibly because of differences in the temperature optima of their carboxylating processes (McWilliiam, 1978).

Net photosynthesis is influenced by the rate of respiration, and dark respiration usually increases steadily with temperature, although the temperature response curves for dark respiration and photorespiration may differ (El-Sharkavy and Hesketh, 1965). Depletion of carbohydrate reserves and a faster aging of leaves were observed when dark respiration was increased by increasing temperatures (Baker and Jung, 1968a, 1968b).

Responses of Tropical Grasses to Water

Seasonal water shortage is the greatest limitation to the growth of C_4 pasture grasses in many areas of the world (Cooper, 1970).

Even on soils at field capacity, transitory leaf water deficits occur daily when atmospheric demand exceed the capacity of water uptake. As the soil dries out the deficits get more severe and more prolonged (Peake et al., 1975).

Plants have developed both morphological and physiological mechanisms to enable them to withstand and adapt to water deficits.

The extent to which water deficits reduce growth and yield by reducing leaf area depends upon the relationship between expansion rate and leaf water potential, both during the stress period and during recovery following rain or irrigation (Hsiao, 1973).

In some instances when plants which are experiencing water deficits are rewatered, their rates of leaf expansion exceed those of well watered plants (Ludlow and Ng, 1976). When deficits are lenient during a short term, the stimulated rates last only a matter of hours, but compensate completely for the reduced elongation during the period

of stress (Kleinendorst, 1975). The degree of compensation tends to disappear as deficits become more severe and in consequence, final leaf area is reduced compared with unstressed plants (Ludlow and Ng, 1977). The rate of leaf expansion in many species declines continuously from high leaf water potentials as water potential declines (Hsiao, 1973).

Ludlow and Ng (1976) reported that leaf elongation rate of Panicum maximum var. trichoglume declined with decreasing water potential, the shape of the response and water potential at which elongation ceased being similar to that found for net photosynthesis measured at high quantum fluxes. These authors also mentioned that net photosynthesis and elongation of P. maximum appear to have similar sensitivities to water stress in contrast with data for other species in which leaf expansion is usually more sensitive than net photosynthesis (Wardlaw, 1969; Boyer, 1970).

Water stress reduced plant growth and delayed stem and flower development of green panic (P. maximum var. trichoglume). The effect on growth resulted from a reduction of both the net assimilation rate and the leaf area ratio (Ng et al., 1975). Reduction in net assimilation rate was the main determinant of lower relative growth rate of stressed plants of green panic over the initial cycles of stress, but subsequently, as leaf area was reduced, leaf area ratio also had a significant influence. Following rewatering, leaf elongation rates of previously stressed plants of green panic exceed those of unstressed plants for periods up to 33 hrs, during which time elongation rate was more related to previous levels of water stress

than to current leaf water potential (Ludlow and Ng, 1977). In addition, there was a transient burst of elongation when plants were rewatered in light.

Several authors (Hsiao, 1973; Kleinendorst, 1975; Ludlow and Ng, 1976) have mentioned that cell division in leaves is less sensitive to water deficit than is cell expansion, in that its rate declines more slowly as water deficit increases and it probably ceases at a lower water potential than cell expansion. Thus, when P. maximum plants were rewatered, stressed leaves would have a larger number of cells available to expand than would unstressed plants and therefore have a higher potential rate of leaf elongation (Ludlow and Ng, 1977). Water stress can also affect leaf area by reducing tillering or accelerating the death of leaves and tillers (Turner and Begg, 1978).

An important physiological mechanism in adaptation of plants to stress is the lowering of osmotic potential. Any loss of water from cells must concentrate the solution within the cell and leads to a decrease in the osmotic potential. In addition to the decrease in osmotic potential due to solute concentration, as water potential decreases, stress may also induce a net solute increase, i.e., osmotic adjustment (Turner and Begg, 1978).

Tropical grasses such as green panic (P. maximum var. trichoglume), buffel grass (Cenchrus ciliaris), speargrass (Heteropogon contortus), and the legume siratro (Macroptilium atropurpureum) are successful species in relatively dry areas of Australia. Their leaf water potentials differ markedly under drought conditions (Peake et al., 1975).

According to Turner and Begg (1978), mechanisms such as leaf hairiness, wax blooms that develop under stress, positive movements of leaves resulting in their orientation parallel to the incident radiation and passive flagging or rolling of leaves when wilted; which reduce the effective leaf area and hence the energy load upon the plant, are of greater benefit to forage species.

Leaf net photosynthesis of _Panicum_ _maximum_ var. trichoglume recovered fully from water potentials as low as -92 bars (Ludlow et al., 1980). The degree of stress experienced during the single drying cycle did not influence the maximum net photosynthetic rate attained during recover, but the time taken to reach the maximum increased with the degree of stress experienced.

Since stomata regulate CO_2 exchange, water deficits that close stomata must also depress photosynthesis (Turner and Begg, 1978).

In green panic (_P._ _maximum_ var. trichoglume) stomatal resistance exerted greater control than intracellular resistance over net photosynthesis in the recovery phase irrespective of the water potential before rewatering or whether plants were preconditioned to stress (Ludlow et al., 1980).

Ludlow and Ng (1976) reported that in green panic the leaf water potential at which net photosynthesis ceased (-12 bars) and stomatal resistance increased substantially (-6 bars) were relatively unaffected by nitrogen supply, environmental conditions during growth, and whether plants had previously experienced stress. However, these factors influenced the rate of net photosynthesis at high water potentials by affecting stomatal resistance and at a moderate water potential by affecting both stomatal and intracellular resistances.

The higher stomatal resistance of C_4 grasses associated with their higher photosynthetic rates under optimum conditions for growth result in better water use efficiency. Indeed, the water use efficiency in C_4 species is twice that of C_3 species (Ludlow and Wilson, 1972; Turner and Begg, 1978).

Supported by the current literature, Turner and Begg (1978) indicated that morphological responses, such as leaf area development, tillering, and root growth are more sensitive to water deficits than physiological processes.

Responses of Tropical Grasses to Light

Light has long been recognized by scientists as a limiting factor in the growth of plant communities. According to Donald (1963) when water and nutrients are in adequate supply, light usually becomes the factor limiting growth or dry matter production. Light is directly required for the photochemical process of photosynthesis and the intensity, quality, and duration of the incident light can affect plant growth and development (Evans et al., 1964; Cooper and Tainton, 1968; Ludlow, 1978). Two biochemical pathways of photosynthesis have been recognized and plants are classified as either C_3 or C_4 species according to the dicarboxylic acid pathway of CO_2 fixation (Hatch and Boardman, 1973; Gifford, 1974; Whiteman, 1980). The largest group of plants having the C_4 pathway are the tropical grasses in the subfamily Panicoideae. Their maximum annual yield recorded is far greater than of temperate grasses and legumes, and tropical legumes, all of which are C_3 species (Whiteman, 1980; Mott, 1983).

The extent to which light is intercepted and how it is distributed over the leaf surface depends upon the canopy architecture and the amount of leaf area available (Cooper and Tainton, 1968; Rhodes, 1973; Ludlow, 1978). In a canopy exposed to full sunlight plant growth increases as light intensity increases up to the point of light saturation of the leaves (Cooper and Tainton, 1968). While leaves of C_3 grasses are light saturated at 30 to 50% of full sunlight, present evidences suggest that leaves of C_4 species are not saturated even in full sunlight (Cooper and Tainton, 1968; Ludlow, 1978). According to Ludlow (1978), leaves of C_4 species do not saturate at full sunlight illuminances because they have lower intracellular and stomatal resistances which decline progressively with increasing illuminance and not because of photochemical and biochemical characteristics of the C_4 syndrome. Photorespiration and the CO_2 compensation point for C_4 grasses are close to zero in the light, whereas in C_3 plants these values are 7 to 15 mg $CO_2/dm^2/hr$ and 40 to 50 ppm, respectively (Mott and Popenoe, 1977; Whiteman, 1980; Mott, 1983).

Tropical grasses potentially have a much higher growth rate than tropical legumes because of their higher rate of photosynthesis (Ludlow and Wilson, 1970, 1972). In general, all components of growth are depressed by a low energy input (Cooper and Tainton, 1968). Indeed, the rates of growth and photosynthesis of C_4 pasture grasses are strongly depressed under shade (Ludlow, 1978). Burton et al. (1959) showed that reduced light decreased herbage yields, production of roots and rhizomes, underground reserves, and total available

carbohydrates in Coastal bermudagrass [Cynodon dactylon (L.) Pers].
Wong and Wilson (1980) noted, however, that the competitive ability of
green panic (Panicum maximum var. trichoglume cv. Petrie) was
intensified under shade to the extent that the proportion of siratro
(Macroptilium atropurpureum cv. Siratro) in a mixed sward declined
from 40% to as little as 4 to 6% when the plants were defoliated every
4 or 8 weeks, and subjected to shading of 60 and 40% of full sunlight.
The competition was most severe in relation to shoot yield, and was
accentuated by shading, frequent defoliation and time. The better
growth of green panic under shade was associated with low levels of
nitrogen supply, because moderate shading stimulates nitrogen uptake
and growth in the grass.

Rhodes and Stern (1978) pointed out that competition for light is
absent or minimal in two situations: in the early stages of an
establishing pasture, where root competition is likely to predominate,
and during the early stages of the regrowth following severe
defoliation. As plants grow, competition for light occurs between and
within plants whenever one leaf or photosynthetically active part, by
its interposition, reduces the light falling on another, thus reducing
the photosynthetic rate.

In the established pasture, the growth habit of the species
involved and the preferential ability of the grasses or legumes to
gain access to light are important factors determining the
productivity and persistence of the pasture (Mott and Popenoe, 1977;
Ludlow, 1978; Wong and Wilson, 1980). Mott and Popenoe (1977) suggest
that in low light environments some tropical legumes and grasses

may have equal competitive ability, assuming the legumes are able to climb to the top of the canopy to expose their leaves to a high level of solar energy.

Other growth-related characteristics of forage plants, such as rate of leaf appearance, tillering and change from vegetative growth to reproductive development are also affected by light intensity and duration (Cooper and Tainton, 1968; Laude, 1972). The influence of day length is frequently related to the initiation of reproductive tillers and flowering. When considering the adaptation of pasture species to particular tropical areas, the photoperiodic response is an important factor to be considered (Whiteman, 1980). Mott and Popenoe (1977) pointed out that the maintenance of grasses in the vegetative stage is usually favorable in sustaining a high nutritive value for grazing animals, as well as preserving high growth rates over a longer period of time.

Developmental Morphology of Forage Grasses

Many forage plants have morphological adaptations that permit them to endure repeated partial defoliation. In order to understand how morphological characteristics affect regrowth after cutting or grazing, one must recall the morphological changes that occur with age during growth and development.

Growth is an irreversible increase in size that is quantitative in nature. On the other hand, development involves qualitative changes in form, structure, and general complexity of the plant. Developmental processes involve cell division, differentiation, and

morphogenesis (Barnard, 1964; Salisbury and Ross, 1978; Wareing and Phillips, 1981).

Growth during germination results mainly from elongation of existing embryonic cells and cell division in specific groups of cells or meristematic regions (Goodin, 1972).

Following seedling establishment there are no basic changes in the plant's structural design and development. The plant grows in size and number of organs but these arise from meristems in which histogenetic patterns are repeated (Goodin, 1972; Jewiss, 1966; Langer, 1972).

Meristems are named according to position in the plant body. Apical meristems occur at the tips of roots and stems (Wareing and Phillips, 1981). Intercalary meristems lie between regions of permanent tissues, e.g., at the base of internodes and at the base of grass leaves (Jewiss, 1966; Dahl and Hyder, 1977). In all grasses, the leaf intercalary meristems remain in a basal position, so that the elevated part of a leaf blade can be removed without stopping growth. Lateral and marginal meristems are also important for the growth and development of plants (Dahl and Hyder, 1977).

In the initial phase of development, leaf primordia arise from a region with high meristematic activity, the apical meristem. Such meristem is also referred to as stem apex, growing point, or sometimes shoot apex (Jewiss, 1966; Langer, 1972). Structures produced by the meristematic tissue contiguous to a leaf primordium forms the phytomer which consists of leaf blade, leaf sheath, internode, axillary bud, and node (Hyder, 1972).

Shoot, or tiller, is a collective term applied to the stem and leaves, or any growing branch in grasses (Langer, 1963; Jewiss, 1966; 1972). One leaf consists of the sheath and the blade (Langer, 1972; Bogdan, 1977). The sheath is the cylindrical, or sometimes compressed, lower part of the leaf which clasps the stem (Langer, 1972; Bogdan, 1977). The blade, usually referred to as leaf, is the linear, lanceolate part of the leaf responsible almost entirely for photosynthesis. The stem is typically divided into nodes and internodes (Bogdan, 1977; Dahl and Hyder, 1977). The nodes are the part of the stem where one or more leaves are attached. Internodes are lengths of stem between two successive nodes.

At the same time that leaf primordia are being formed, other meristematic tissues, the axillary buds, arise in the axil of each leaf throughout the stem. Some time later basal buds may develop at ground level (Jewiss, 1966). Under suitable conditions these buds may germinate originating axillary shoots, or tillers, which are similar in structure to the shoot from which they arise (Langer, 1963). The leaves of tillers also subtend axillary buds which in turn may form other tillers. Shoots from the main stem are usually referred to as primary tillers, shoots produced from them are called secondary tillers, and so on (Langer, 1963; Jewiss, 1972).

Tillers growing upwards within the enveloping leaf sheath are called intravaginal tillers and are typical of plants with a tufted or bunch type growth habit. Tillers that break through the leaf sheath are called extravaginal tillers and are common in plants with spreading or creeping growth habits (Langer, 1963, 1972; Jewiss, 1966;

Dahl and Hyder, 1977). The latter are also called stolons, if they are growing horizontally above the ground surface, and rhizomes if below.

When leaves are first formed they occur close together, and nodes and internodes are, or appear absent (Jewiss, 1966; Dahl and Hyder, 1977). Subsequently, by differentiation, cells of apical meristem can cause the elongation of internodes, and promote stem growth (Jewiss, 1966).

Stem growth is important in determining the ability of forage plants to gain preferential access to incident radiation under circumstances of competition for light. Stem growth also influences the number and position of apices which in turn determine the number of growing points that remain after defoliation. In grasses, stem growth is associated with flowering, increase in the height, change in canopy structure, and possibly with decline in nutritive value (Ludlow, 1976).

Morphology and Responses of Grasses to Grazing

To a great extent the responses of forage grasses to grazing depend on their growth habit. Differences in habit among grasses are due to the pattern of lateral shoot development and the length of stem internodes (Jewiss, 1966). The elongation of internodes reduces the density of buds close to the ground, elevates the canopy, and increases apical meristems vulnerability to cutting or grazing (Branson, 1953; Booysen et al., 1963; Gomide, 1973; Humphreys, 1981). Thus, the position of the growing points at the time of cutting or

grazing is an important morphological factor in determining susceptibility of forage plants to defoliation (Booysen et al., 1963; Jewiss, 1966; Langer, 1972; Gomide et al., 1979; Dovrat et al., 1980; Humphreys, 1981).

In most of the temperate grasses the internodes do not elongate during the vegetative phase of growth. In such plants the apical meristem continues to produce new leaves until differentiation to reproductive stage occurs (Jewiss, 1966).

In tropical grasses stem elongation may occur while the plant is still in the vegetative phase of growth. Thus the apical meristems are elevated and become vulnerable to cutting or grazing (Booysen et al., 1963; Gomide, 1973). Furthermore, lack of capacity of a tiller to regrow after cutting is mainly caused by the removal of the apical meristem with defoliation (Gomide, 1973; Dovrat et al., 1980). In addition, grazing below the apical meristem stops stem elongation and prevents leaf replacement from that stem except by the process of tillering from buds of the crown (Langer, 1963, 1972; Jewiss, 1966, 1972; Humphreys, 1966, 1981).

Tillering

The tiller is the basic vegetatative unit of grasses, and tiller number and size have been used to analyze grass growth. Tillering in grasses has been reviewed by Langer (1963), Laude (1972), and Jewiss (1972).

The life story and longevity of tillers may vary with time of origin and environment. Langer (1963) distinguished three types of tillers: a) tillers which flower and consequently die in the year of their appearance thus describing an annual life cycle, b) those which flower and die in the year following their formation in the manner of a biennial plant, and c) tillers which fail to flower and whose length of life could vary from a few weeks to a year or more.

The question of whether tillers function as independent units or whether they are physiologically dependent is always asked, and still constitutes an interesting field of research. Tracer studies conducted by Marshall and Sagar (1965) and Gifford and Marshall (1973) have shown that the grass plant is a highly organized and fully integrated system rather than a collection of competing individual tillers.

Inhibition of tillering or suppression of axillary bud development, due to apical dominance, have long been recognized in grasses (Leopold, 1949). It is well known that auxins play the main role but the hormonal mechanisms of action involved still are uncertain (Sosebee, 1977). Other hormones as well as hormonal interactions, such as auxin-gibberellin interactions, may be involved in the growth-promoting process (Wareing and Phillips, 1981). Sachs and Thimann (1967) suggest that auxin diffuses from the apex down the stem into the lateral buds, inhibiting their growth and development. Therefore, removal of the apical meristems cause the lateral and basal buds to be activated and begin elongation and growth (Goodin, 1972).

Tillering is explained not only on the basis of apical dominance, but seems also related to genotype and environmental factors. In general, tillering is reduced by water stress (Turner and Begg, 1978) and a rise in temperature, fall in light quantity, or partial defoliation can induce bud inhibition (Langer, 1963; Laude, 1972). Season of the year and mineral nutrition can also affect the rate of tillering in tropical grasses (Pedreira, 1975; Beaty et al., 1977).

Dahl and Hyder (1977) indicated that tillering ability from axillary buds without the apical meristem being removed is considered an indication of an efficient forage producer. During growth of a controlled sward, the dry matter yield of shoots increases because of both the weight increase of individual tillers and the increase in number of tillers (Humphreys, 1966, 1981; Dovrat et al., 1980). However, the rate of tiller initiation in the pasture environment may be significantly affected by grazing.

Youngner (1972) concluded that, when defoliation removes apices of elongated stems, apical dominance is broken and the rate of tiller production is increased. On the other hand, defoliation that removes only leaves usually leads to decreased tillering (Youngner et al., 1976; Ackerson and Chilcote, 1978). One possible explanation is the fact that available carbohydrates are used for leaf growth in existing tillers before being used to support new tiller growth (Youngner, 1972). In closed canopies under field conditions, defoliation may enhance tillering even when apices remained undamaged. This could result from a more favorable light environment, created by reduction of shading, which would be expected to stimulate tillering (Jewiss, 1972; Laude, 1972; Youngner, 1972).

Although it has been indicated that grazed tillers become dependent upon ungrazed tillers for photosynthate used in regrowth (Gifford and Marshall, 1973; Dyer et al., 1982), under some circumstances tillers die.

The causes of tiller death, excluding those due to predation, drought, cold, and disease are not completely known. In temperate grasses, tiller death may occur at any time of the year but a high proportion of tiller death has often been reported to occur during early reproductive growth (Langer et al., 1964). It has been suggested that nutrient stress (Aspinall, 1961) and shading (Bean, 1964) may also be responsible for plant and tiller death in the sward. It has been observed that at a time of environmental stress many young vegetative tillers tend to die soon after they have appeared (Langer, 1972).

Other studies have shown that the time of tiller origin is crucial to the survival of tillers (Wilson, 1959; Hill and Watkin, 1975). Ong (1978) provided experimental evidence that tiller death can be induced on a vegetative ryegrass plant (Lolium perenne L., cv. S23) by subjecting the whole plant to either nutrient stress, low light intensity, or both. He noted as well that the dead tillers were smallest and often, but not always, the youngest on the plant.

Ong et al. (1978) reported that physiological causes accounted for most tiller deaths in a 2-year old sward of perennial ryegrass (L. perenne L., cv. S23) between April and August. Using $^{14}CO_2$ and selective defoliation, they showed that in April defoliated tillers imported radiocarbon from undefoliated tillers but that in July at

anthesis an undefoliated tiller retained most of the carbon it fixed, despite its vascular association with defoliated tillers. They suggested that much of the tiller death was due to the failure of the large flowering tillers to support the growth of the young vegetative tillers which are dependent on imported assimilates, nutrients, and water for their growth and survival.

<u>Leaf Senescence</u>

Senescence in plants encompasses all processes of deterioration that accompany aging and that lead to death of an organ or of the whole plant (Salisbury and Ross, 1978; Wareing and Phillips, 1981). In many plants each leaf has only a limited life span so that as the shoot continues to grow in height the older basal leaves tend to senesce and die progressively. This pattern of senescence is called sequential senescence and it must be distinguished from the simultaneous senescence that occurs in temperate deciduous trees in which all leaves senesce and die at about the same time of the year (Wareing and Phillips, 1981). Leaf senescence is accompanied by early losses in chlorophyll, RNA, and proteins. The first visible sign of senescence is yellowing of the leaf, due to break down of chlorophyll which makes visible other leaf pigments, particularly the xanthophylls and carotenoids (Salisbury and Ross, 1978; Wareing and Phillips, 1981). Sequential leaf senescence seems to be caused by competition for metabolites and nutrients between old leaves at the base of the stem and young growing leaves in the apical regions. There is evidence indicating that senescence is also hormonally controlled

(Brady, 1973). Thus, the rate of senescence of plant organs is often under control of the whole plant. In addition to internal factors of the plant which are involved in the regulation of senescence, a number of external factors may affect the rate of senescence, including drought, mineral nutrition, disease, light intensity and length of the day (Pearce et al., 1965; Hopkinson, 1966; Laude, 1972; Brady, 1973; Wilson and Mannetje, 1978). Hopkinson (1966) suggests from his studies that rate of leaf senescence is accelerated by shading. On the other hand, Woledge (1971) found that old leaves of large tillers and leaves of small shaded tillers increased their photosynthetic rate when they were exposed to light and thus became useful to the growth of the sward. Grant et al. (1981) noted that senescence was increased by reduced light penetration and higher proportion of more aged tissue in both cut and grazed _Lolium_ _perenne_ swards. Senescence, death, and decay of plant material situated at the bottom of the sward have been associated with moisture status of the soil (Hunt, 1965, 1971). In general, water stress accelerates the death of old leaves but the time when stress occurs and the stage of development of the leaf are also related to senescence rate in tropical grasses (Ng et al., 1975; Wilson and Mannetje, 1978). Senescence rate is also influenced by ontogenetic variation within the tiller due to leaf positional effects (Wilson, 1976). Indeed, Wilson and Mannetje (1978) found that in buffelgrass (_Cenchrus_ _ciliaris_ cv. Bileola) and green panic (_Panicum_ _maximum_ var. trichoglume cv. Petrie) leaves of high insertion level produced in the autumn on well-developed tillers had slower senescence rates than the early leaves produced on new tillers in the spring.

Wilson and Mannetje (1978) pointed out that because animals selectively graze leaves, investigation of the rate of leaf development and senescence, as well as changes in the composition and digestibility of leaves, would be particularly valuable for understanding pasture changes affecting feed quality.

Morphology of Tropical Grasses and Regrowth Relationships

It has been shown that the regrowth of many tropical grasses is closely related to the fate of apical meristems following defoliation (Andrade and Gomide, 1971; Tardin et al., 1971; Nascimento Jr. and Pinheiro, 1975; Gomide et al., 1979; Dovrat et al., 1980). However, differences may occur among species of a single genus. For example, Pennisetum americanum failed to regrow subsequent to tiller decapitation during the internode-elongation stage of crop growth (Begg, 1965), while hybrid Pennisetum (P. americanum X P. purpureum) did regrow after tiller decapitation (Muldoon and Pearson, 1979a). The regrowth of elephantgrass was found to be closely related to the survival of the apical meristems (Andrade and Gomide, 1971).

Tardin et al. (1971) found a close correlation among apical meristems eliminated and regrowth in Guatemalagrass (Tripsacum sp.). Only 28.5% of the apical meristems were eliminated when plants 147 days old were cut at ground level. Considering that the apical meristems remained close to the ground for a long period of time, the authors concluded that cutting height is more important for the latter species than for elephantgrass.

The vegetative development of jaraguagrass [Hyparrhenia rufa (Nees) Stapf.] following germination until flowering was studied by Nascimento Jr. and Pinheiro (1975). They observed that this grass did not show any visual sign of morphological differentiation until 84 days of age. The earliest morphological change indicating transition from vegetative to reproductive stage was the elongation of the apex. After 84 days of age, large variations in the regrowth were observed due to the elevation of apical meristems and their consequent elimination.

Variation in number of basal buds per tiller, tillers per crown, height of apical meristems, and content of nonstructural carbohydrates in stem bases as affected by plant age, height of cutting, succession of growth, and intervals between growth were studied in coloniaograss (Panicum maximum Jacq.) during the growing seasons of 1974-75, 1975-76, and 1976-77 by Gomide et al. (1979). The authors observed that height of apical meristems increased with fertilizer application, growth order, extension of clipping intervals, height of cutting as well as plant age. Therefore, for a given height of cutting, more apical meristems were eliminated in older plants at the time of clipping. As a consequence, the dry matter of regrowths recorded 21 days after cutting were drastically affected.

One interesting observation in the above mentioned experiment was that successive low clippings, taken at the same plant age, did not necessarily result in higher elimination of apical meristems since such management tends to lower the height of stem apices. This fact suggested that plants can modify their growth habit under different situations of management.

Garcia and da Silva (1980) noted that the apical meristems of buffel grass (<u>Cenchrus</u> <u>ciliaris</u> L.) showed up very early, reaching 24.3 cm with 42 days of growth. They suggested that buffelgrass should be cut or grazed after 56 days of growth in order to get the maximum dry matter production. Although many growing points can be removed by grazing after 56 days, enough carbohydrate reserves would be stored and new tillers would be stimulated by lack of apical dominance.

A tendency for early stem elongation was also observed in Rhodesgrass (<u>Chloris</u> <u>gayana</u> Kunth.) by Dovrat et al. (1980). The lack of capability of tillers to regrow after cutting was closely related with developmental stage of tillers. Thus, the relatively small number of sites available for regrowth was considered as a major deterrent for fast shoot growth of a Rhodesgrass sward after defoliation.

Carbohydrate Reserves in Forage Plants

Historically, the importance of carbohydrate reserves goes back to the 1920s when Graber et al. (1927) defined organic reserves as those carbohydrates and nitrogen compounds elaborated, stored and utilized by the plant itself as food for maintenance and the development of future top and root growth. Since then, and especially in the last 30 years, an overwhelming quantity of carbohydrate studies have been published in an effort to elucidate the role of carbohydrate reserves in the growth and regrowth of forage species (Weinmann, 1952,

1961; Troughton, 1957; May, 1960; Smith, 1972, 1973; Sheard, 1973; White, 1973; Trlica, 1977; Deregibus et al., 1982).

It has been generally accepted that reserve substances consist largely of carbohydrates. Smith (1969) suggested that the term total available carbohydrates should be replaced by total nonstructural carbohydrates as a more definable term to both plant and animals investigators.

Nonstructural carbohydrates are defined as those carbohydrates stored in the more permanent organs of the vegetative-reproductive system of the plant as a readily available source of energy that can be utilized by the plant itself to start new growth, or to insure survival after defoliation or periods of climatic stresses (Smith, 1972, 1973; White, 1973).

Forage grasses fall into two groups according to the type of nonstructural carbohydrates accumulated in their vegetative tissues. While grasses of temperate origin store predominantly fructosans, grasses of tropical and subtropical origin accumulate starch (Smith, 1968; Ojima and Isawa, 1968; Hunter et al., 1970; Smith, 1972; White, 1973). Other sugars, such as monosaccharides and sucrose are also found in vegetable tissues but they are largely metabolic intermediates and generally occur in low concentration (Weinmann, 1961; McIlroy, 1967; Smith, 1972, 1973). Fats, oils, and nitrogen compounds may also be synthesized, translocated, and stored within plants but their importance as readily available sources of energy for metabolism in vegetative plant parts is considered to be of lesser importance (Trlica, 1977; Deregibus et al., 1982).

Smith (1972) pointed out that a knowledge of the level of reserve carbohydrates and information on periods of storage and utilization are important to cutting and grazing management practice since this will indicate the potential of plants to regrow after defoliation. In this context an estimate of total nonstructural carbohydrates would be more practical, rather than an estimate of each individual fraction (Smith, 1969, 1973). The principal methods for analysis of carbohydrates in species accumulating starch have been those using acid or enzymatic hydrolysis (Smith, 1973). Recently, an adaptation of methods in which enzymatic hydrolysis is followed by colorimetric determination was discussed and proposed by Christiansen (1982).

Almost as important as the method of analysis of carbohydrates are the storage organs which are stem bases, stolons, rhizomes, tubers, crowns, and roots (Troughton, 1957; Deregibus et al., 1982). It has been indicated that in perennial grasses the stem bases constitute a major storage organ (Smith, 1972; Noble and Lowe, 1974).

Nonstructural carbohydrates may be temporarily stored in all plant parts following a well known pattern of use and storage. Accumulation of reserves occurs when assimilates produced by photosynthesis are in excess of demands for maintenance, growth and reproduction. During regrowth, or at any time when photosynthesis is not enough to meet the demands of the plant, the reserves may be redistributed by three processes: respiration, translocation to new root growth, and translocation to new shoot growth (Sheard, 1973).

Early investigations showed that following defoliation there is always an associated decrease in the carbohydrate reserves of the

plants (Sullivan and Sprague, 1943; Sprague and Sullivan, 1950;
Reynolds and Smith, 1962; Eastin et al., 1964). These observations
have led to the general belief that reserves are incorporated into new
tissue during regrowth.

Although some researchers have questioned the role of reserve
carbohydrates in regrowth of plants (May, 1960; Jameson, 1963;
Davidson and Milthorpe, 1965a, 1966), the works of Pearce et al.
(1969) and Smith and Marten (1970) with ^{14}C have firmly established
the importance of organic reserves in the storage organs of forage
plants as a material that is mobilized and utilized for respiration
and synthesis of new tissue during regrowth.

The level of nonstructural carbohydrates in storage organs of
plants is constantly changing. Cyclic fluctuations, daily and
seasonal, in the level of carbohydrates have been related to climatic
factors, to developmental stages within the plant, to mineral
nutrition, and to frequency, intensity, and time of defoliation
(Humphreys, 1966; White, 1973; Trlica, 1977; Harris, 1978; Deregibus
et al., 1982). Usually, conditions that promote growth or regrowth
tend to reduce carbohydrate reserve levels in forage plants.

The effects of temperature on carbohydrate reserves varies
according to the origin of the grass species (Wilson and Ford, 1973;
Noble and Lowe, 1974). In general, low night temperatures favor the
accumulation of carbohydrates whereas temperatures that stimulate
growth induce a depletion of reserve substances (Brown and Blaser,
1965, 1970; Blaser et al., 1966; Wilson and Ford, 1973; Ferraris,
1978; Deregibus et al., 1982). When day/night temperatures were

increased from 21/16 to 30/25°C, nonstructural carbohydrates in the
stubble of elephantgrass decreased from 8 to 5% and the dry matter
yield per pot increased from 41 to 200 g (Ferraris, 1978).

In response to water stress, forage plants tend to increase the
level of carbohydrate reserves in the storage organs (Brown and
Blaser, 1965, 1970; Blaser et al., 1966; Trlica, 1977; Ludlow et al.,
1980). Ludlow et al. (1980) found that nonstructural carbohydrates in
green panic (Panicum maximum cv. trichoglume) subjected to water
stress was three to four times higher when compared with well watered
plants. Although under water stress stomata tend to close, it was
observed that osmoregulation of stomatal opening occurred when the
water stress was slowly developed, thus allowing some photosynthetic
activity.

Fertilization, especially nitrogenous, may have a marked effect
on the level of carbohydrate reserves in forage plants, given that
other nutrients and environmental factors do not limit plant growth.
Nitrogen applied at low levels or deficiency of soil nitrogen cause
the accumulation of sugars in the plant. On the other hand, an excess
in the level of nitrogen available to the plant stimulates the
synthesis of protein and prevents the accumulation of carbohydrates as
reserves (Adegbola and McKell, 1966; Dovrat and Cohen, 1970; Dovrat et
al., 1972; Trlica, 1977; Deregibus et al., 1982).

Differences among tropical grasses in the period of time
necessary for reserve reestablishment were noted by Nascimento et al.
(1980). Nonstructural carbohydrates of stem bases decreased during
the first 7 days of regrowth and were recovered after 21 days

of regrowth in guineagrass (Panicum maximum), after 21 to 35 days in molassesgrass (Melinis minutiflora), and after 49 days in jaraguagrass (Hyparrhenia rufa).

If the importance of nonstructural carbohydrates is assumed, at least to maintain the respiration of the root system, it becomes evident that under grazing conditions different periods of rest must be observed for each species in order to ensure survival of the plants and persistence of the pasture.

Nonstructural Carbohydrates and Regrowth Relationships

It has been suggested that an adequate level of reserve carbohydrates is important in determining the regrowth rate of forage swards as well to allow the plants to withstand stress conditions (Smith, 1972, 1973; Youngner, 1972; Sheard, 1973; White, 1973; Vickery, 1981; Deregibus et al., 1982).

Association between the level of reserves and regrowth following defoliation or a dormancy period has been demonstrated with forage species (Ward and Blaser, 1961; Okajima and Smith, 1964; Eastin et al., 1964; Adegbola and McKell, 1966; Smith and Silva, 1969; Greub and Wedin, 1971). In general, the rate of regrowth was slower and the amount of regrowth was less for plants with lower carbohydrate reserves. However, the results of some investigations with tropical and subtropical grasses have indicated that the regrowth of these species after defoliation is mutually dependent on the morphological development of the plants, level of reserves and residual leaf area (Humphreys and Robinson, 1966; Gomide et al., 1979; Dovrat et al., 1980; Jones and Carabaly, 1981).

Barnes (1961) observed that frequent cuts in Sabi Panicum, a cultivar of _Panicum maximum_ Jacq., decreased the dry weight and the amount of carbohydrates in the root system. Thus, the subsequent regrowth was affected. This result was further confirmed by Barnes and Hava (1963). On the other hand, Gomide et al. (1979) found that dry matter yields of coloniaograss (_P. maximum_ Jacq.), after clippings taken at different ages, did not appear to be affected by nonstructural carbohydrates. The content of carbohydrates of the stem bases decreased as the plant aged during the establishment phase and only toward the end of the grazing season showed an increase with plant age. Lower values of total nonstructural carbohydrates were observed in fertilized plants as well as during early regrowth after clipping. Similar results were found by Gomide and Zago (1980).

The amounts of total nonstructural carbohydrates in the shoot, stubble, and roots of Rhodesgrass (_Chloris gayana_ Kunth.) are relatively low when the grass is grown under conditions which favor rapid growth (Dovrat and Cohen, 1970; Dovrat et al., 1972). When plants of cultivar Katambora were subjected to different lengths of precutting periods and cutting intervals, it was noted that the availability of total nonstructural carbohydrates in roots and stubble could hardly be the major cause for slow initial regrowth of the sward after the long pre-cutting period (28 days) compared with the short (7 days) pre-cutting period (Dovrat et al., 1980).

The effects of clipping height and burning on regrowth of 12 tropical grass accessions were evaluated by Jones and Carabaly (1981). Regrowth potential (regrowth in the dark) in 11 accessions was not

correlated with actual regrowth or relative growth rates during the first 3 weeks.

The effects of intensity of defoliation (0, 50, and 100% of leaf area left after defoliation) on the regrowth of dwarf elephantgrass plants with 28, 56, and 84 days of age was studied by Castillo-Gallegos (1983). He found that age of the plant at defoliation appears to be more important than total nonstructural carbohydrates in stem bases in determining the relative growth rate of the regrowth.

The poor correlation found between carbohydrate reserves and regrowth rates in many species may well be explained by the simultaneous utilization of other organic compounds as source of energy for regrowth. On the other hand, the hypothesis that reserve carbohydrates are only utilized during the first days of regrowth and that later regrowth is dependent on leaf area and photosynthesis cannot be disregarded (May, 1960; Jameson, 1964; Davidson and Milthorpe, 1965a, 1965b, 1966; Youngner, 1972; Sheard, 1973; Trlica, 1977; Humphreys, 1966, 1981; Deregibus et al., 1982).

Light Utilization, Leaf Area, and Regrowth Relationships

The interrelationships of light and leaf area for rapid regrowth and high yields of forage plants have been reviewed by several authors (Donald and Black, 1958; Donald, 1963; Humphreys, 1966; Brown and Blaser, 1968; Wilson, 1973; Ludlow, 1978). Interest in these relationships was stimulated when Watson (1947) placed them on a quantitative basis defining the concept of leaf area index (LAI) as

the ratio of leaf area (one surface) to unit of area of the soil occupied by the plants. The critical or optimum LAI is the point where 95% of the incident light is intercepted and the maximum crop growth rate is attained (Donald and Black, 1958; Donald, 1963; Humphreys, 1966; Youngner, 1972). The LAI varies from 2 to 3 to over 15 among species, and there are also large differences among varieties within species (Mott and Popenoe, 1977). The LAI *per se* does not stabilize at an optimum and may increase as the plant continues to grow. In some circumstances the maximum growth rate is maintained with further increases in LAI, but in others a decline occurs due to increased shading and respiratory load at the base of the canopy (Rhodes, 1973; Humphreys, 1981; Crowder and Chheda, 1982).

Despite some limitations in the use of LAI concept in pasture management, which arise mainly from changes in photosynthetic characteristics, canopy architecture, or botanical composition, Brown and Blaser (1968) concluded that LAI related to light interception appears to be a useful tool for understanding forage growth and developing better varieties and management practices.

References dealing with values of light interception and LAI of subtropical and tropical grasses under cutting or grazing conditions are few. In general, it has been indicated that the pasture should be managed in such a way as to leave an adequate residual LAI for continued or rapid renewal of growth (Brougham, 1956; Ward and Blaser, 1961; Alexander and McCloud, 1962; Humphreys, 1966; Humphreys and Robinson, 1966; Brown and Blaser, 1968; Youngner, 1972; Ludlow and Charles-Edwards, 1980; Jones and Carabaly, 1981). Although the

maintenance of an optimum LAI under grazing conditions is practically impossible; it is recognized that reduced growth will occur at lower values of LAI because of inadequate light interception, and at higher LAI values because increased respiratory activity and accelerated senescence of leaves (Humphreys, 1966; Brown and Blaser, 1968).

One of the earliest studies relating light interception by the pasture sward to the amount of leaf area present was reported by Brougham (1956). He subjected a sward of short rotation ryegrass (Lolium perenne L. X L. multiflorum Lam.), red clover (Trifolium pratense L.), and white clover (Trifolium repens L.) to three different intensities of defoliation. Where the defoliation height was 2.5 cm, light interception was almost complete (95% or over) 24 days after cutting, whereas swards defoliated to 7.5 and 12.5 cm intercepted almost all the incident light 16 and 4 days after cutting, respectively. The more intense the defoliation the lower was the initial rate of regrowth, but maximum growth rate in all treatments was reached when 95% of the light was intercepted.

Ludlow and Charles-Edwards (1980) analyzed the regrowth of Setaria anceps/Desmodium intortum swards cut to 7.5 or 15 cm and defoliated every 3 or 5 weeks. Photosynthetic and respiratory characteristics of the swards were not significantly affected by intensity or frequency of defoliation and the main differences in canopy photosynthesis resulted from differences in light interception. The main effects of height and frequency of defoliation on dry matter production were through their effects on LAI and light interception.

Indeed, dry matter production during the experiment increased with cutting height and with interval between defoliations, and the proportion of grass to legume was unaffected. They concluded that where height and frequency of defoliation have a small effect on leaf photosynthetic characteristics, their effect on pasture regrowth can be quantitatively described by LAI and light interception.

The effects of clipping height and burning on 12 tropical grass accessions were evaluated by Jones and Carabaly (1981). Correlations were determined to study the influence of residual LAI or residual dry matter upon the relative growth rate and dry matter yield of the regrowth in six cultivars, including stoloniferous (Brachiaria mutica, B. decumbens, B. radicans) and caespitose species (Andropogon gayanus, Panicum maximum, P. maximum cv. Makueni). They concluded that the maintenance of an adequate standing crop, avoiding excessive defoliation in tropical grasses with a caespitose growth habit, is an important factor in the maintenance of adequate regrowth. Residual leaf area and residual dry matter were correlated with the regrowth during the first 3 weeks after clipping when stoloniferous and caespitose accessions were considered separately.

Morphology and Physiology: One Approach to the Management of Elephantgrass

It has been the general experience among forage researchers that more frequent and more intensive defoliation of pasture plants result in reduction of the stand, vigor, and herbage dry matter yields. Indeed, elephantgrass cut at 28-day intervals produced less dry matter than when cut at 56- or 84-day intervals (Patterson, 1933; Vieira and Gomide, 1968).

Blaser et al. (1955) indicated that the stand of elephantgrass can be maintained well, provided there is a short grazing period of 5 to 10 days and a recovery period of 20 to 30 days after each grazing period. In order to achieve an efficient utilization of the forage produced and persistence of the pasture, they emphasized the importance of a rotational grazing system with five paddocks. In this system a grazing period of 5 to 7 days would allow the consumption of 90% of the herbage produced by plants which were allowed a rest period of 20 to 28 days.

Studying the effects of three cutting heights (1-3, 30-40, and 70-80 cm) on elephantgrass, Werner et al. (1965/1966) observed that increasing the intensity of defoliation decreased dry matter yields. They suggested that the morphology of the plant should be considered in the management of this grass.

In an uninterrupted growth study of elephantgrass, Pedreira and Boin (1969) found that the number of tillers per area decreased markedly after 42 days of age. The plants were allowed to grow until 210 days, and it was observed that the highest dry matter yield occurred when plants were cut at 105 days and that the ratio of leaf to stem decreased with age.

Andrade and Gomide (1971) cut elephantgrass plants from 28 to 196 days of age at 28-day intervals, and recorded the regrowth dry matter yields after 28 days. They observed a rapid and early stem elongation, so that all apical meristems were eliminated when the cut was made at 56 days of age. Higher dry matter yield was obtained when the grass was cut after only 28 days, because the survival of apical meristems engendered good regrowth.

The intensity of defoliation can affect the characteristics of new tillers. Thus, Belyuchenko (1980) observed that the height of cutting modified the proportion of new tillers in the regrowth of elephantgrass. When plants were cut close to the ground, tillers originated from buds on the rhizome. Cuts at 10 or 15 cm produced an appreciable number of basal buds arising from the crown tillering area. Cutting at 15 cm or higher led to a predominance of aerial tillers arising from axillary buds on the stems.

The interactions between environmental conditions and responses to nitrogen were observed in an experiment carried out by Muldoon and Pearson (1977) with hybrid _Pennisetum_. Production was markedly seasonal. Leaf area responses to season and nitrogen resulted from changes in individual leaf size, leaf number, and the leaf area/leaf weight ratio.

The effects of photoperiod and temperature on the first growth and regrowth of elephantgrass was studied by Ferraris (1978) under controlled environment and under field conditions. In phytotron cabinets, higher temperatures (30/25°C day/night) during early growth induced a more rapid rate of leaf appearance, more rapid stem growth, and more rapid tillering, when compared to lower temperatures (21/16°C day/night). The 16-hour photoperiod resulted in higher yields at harvest than the 8-hour photoperiod. Plants grown at higher temperatures, produced higher leaf, stem, and total dry matter yields, greater leaf area but lower carbohydrate content in the stubble when harvested with 60 days. In the field, similar results to the phytotron experiment were obtained; more tillers and higher yields were obtained in the regrowth. The authors concluded that low

temperatures rather than photoperiod is the main limitation to the adaptation of elephantgrass when year-round production is required.

Muldoon and Pearson (1979a) concluded that in hybrid _Pennisetum_ a faster increase in shoot weight during regrowth, when compared with primary growth, is due to rapid tillering and enhanced rate of leaf appearance after defoliation.

Muldoon and Pearson (1979b) observed that the regrowth of decapitated plants of hybrid _Pennisetum_ was delayed until the development of new tillers, after which new growth was very rapid. When the apical meristems were left intact, initial regrowth was more rapid at the expense of losses in stem dry weight.

Regrowth yield was found to be significantly and positively correlated with tiller density, both in the parent crop at harvest and in the regrowth crop of elephantgrass (Ferraris and Sinclair, 1980a). They noted as well that the stem height was strongly associated with both total and stem dry matter yields in elephantgrass (Ferraris and Sinclair, 1980b). A seasonal retardation in growth rate was associated with moisture, thermal, and energy parameters of the climate.

The current literature suggests that the ability of a pasture plant to survive and produce forage under grazing cannot be explained on the basis of morphology, leaf area residual or reserve carbohydrates alone. Further, morphological and physiological responses of pasture grasses are closely related to environmental conditions. Many years of research are needed to integrate all these separate factors together into a practical and efficient guide leading to a more efficient system of forage production.

Response Surface Methodology in Grazing Experiments

Grazing trials are expensive to run and require long-term experimentation in order to allow ultimate conclusions to be drawn. In addition, grazing experiments require large land areas and consume appreciable amounts of time, labor, and supplies. The number of treatments that can be evaluated simultaneously is frequently restricted by the availability of adequate animals.

It has been suggested that investigations on better management practices must continually receive high priority in forage research if farm profits are to remain reasonably high and agricultural products cheap (Morley, 1978). The dynamics of the grazing environment, i.e., plants, animals, and their interaction, along with the nature of treatment combinations to be studied (e.g., stress on plants associated with frequency and intensity of defoliation) determine which measurements are appropriate and necessary. At the same time, sufficient precision is needed to identify some difference which is considered biologically or commmercially important. Some combination of different types of measurements will maximize the benefits flowing from the resources available and a fast turnover of research-related information demand designs in which the estimation of response surfaces will replace the testing of null hypothesis (Morley, 1978).

According to Balaam (1975), four types of experimental designs may provide useful information for response surface analysis: complete factorial, fractional factorial, central composite, and rotatable designs.

Complete factorials represent one statistical approach to understand complex relationships among experimental factors (Steel and

Torrie, 1980). However, an experimental explosion of treatment combinations associated with an increase in the number of factors or levels of factors frequently restrict their use in agricultural experimentation (Balaam, 1975). Fractional factorials constitute some improvement in reducing the size of the experiment but extreme care is required with regard to effects of confounding (Cochran and Cox, 1957).

Central composite designs were introduced by Box and Wilson (1951) to decrease the larger number of treatment combinations necessary in factorial experiments. These designs were originally developed to be used in areas of experimentation where the length of each study is relatively short, the experimental material does not have high variability and is adaptable to sequential study (Balaam, 1975; Box et al., 1978; Mott, 1982). The first applications were in chemical and engineering fields. In the last 20 years an increasing number of biological related experiments have been analyzed using response surface methodology (Hill and Hunter, 1966; Mead and Pike, 1975). The theoretical procedures used in response surface analysis have been described by Myers (1971) and Box et al. (1978).

In some situations the central composite designs may be modified in order to accomodate treatment combinations that better fit a particular field of research. Such is the case presented by Littell and Mott (1975) where a more complete coverage of the response surface of agronomic studies can be obtained by adding design points at the extreme of the experimental variables.

The application of response surface methodology to forage-livestock experiments has been suggested to reduce the magnitude of

grazing trials as well as to estimate optimum operating conditions when multiple factors are studied in combination (Mott, 1982).

Mott (1982) proposed the use of a modified central composite design in the last phase of an evaluation scheme for screening forage germplasm and his approach is supported by the research of his graduate students (Maraschin, 1975; Serrao, 1976; Santillan, 1983; Veiga, 1983). A modified central composite design was used by Maraschin (1975) and Serrao (1976) to study the effects of grazing pressure, days of rest on a mixture of 'coastcross-1' bermudagrass [Cynodon dactylon (L.) Pers.] and 'Greenleaf' desmodium [Desmodium intortum (Mill.) Urb.]. The response variables analyzed in their study included: forage yield, forage quality, and botanical composition of the pasture. Santillan (1983) studied a tropical grass-legume mixture in Ecuador using a modified non-rotatable central composited design. The experimental variables imposed at five levels each were: days grazing, days rest, grazing pressure, and phosphorus fertilizer. The scope of the experiental range was increased by the addition of eight treatment combinations in the corners of the design. Veiga (1983) analyzed quantitative and qualitative data collected concurrently in this experiment using a second order polynomial model.

Box et al. (1978) stated that graphical summaries and contour plots, being more digestible for most people than mathematical equations, are more understandable in reporting response surface studies. For this purpose, the procedures used in the development and analysis of computer graphics have been given by Schoney et al. (1981).

MATERIALS AND METHODS

General Description

This study was conducted from April to November 1982 at the Beef
Research Unit (BRU) of the University of Florida which is located
about 20 km northeast of Gainesville, Florida (30°N latitude and
82°5'W longitude). The area is a typical flat pine land commonly
called flatwoods. The native vegetation, mentioned by Koger et al.
(1961), consisted primarily of longleaf pine (_Pinus australis_ Michx.
f.), wiregrass (_Aristida_ spp. and _Sporobulus_ spp.), saw palmetto
(_Serenoa repens_ Bartr. Small), galberry (_Ilex glabra_ L.), runner oak
(_Quercus minima_ Sarg.) and cypress (_Taxodium asendens_ Brongn.). The
area was originally cleared and pastures were established in 1952.
Presently, Pensacola bahiagrass (_Paspalum notatum_ Flugge.) is the
dominant grass in most pastures in the area.

The climate is subtropical and humid with an average annual
precipitation of 1300 mm and a frost-free period averaging 276 days
(USDA, 1954). The climatological data recorded at the BRU for 1980,
1981, and 1982 and the rainfall normal values for the Gainesville area
are given in Table 1.

In general, the soils of the BRU are of low fertility and vary
from moderately well drained to very poorly drained (Koger et al.,
1961). According to USDA (1982) most of the soil at the experimental
site is an Entisol classified as Chipley series (thermic, uncoated,

Table 1. Climatological data at the Beef Research Unit and normal rainfall for Gainesville, Florida.

| | 1980 | | | 1981 | | | 1982 | | | Normal* Rainfall |
| | Temperature Max | Min | Rainfall | Temperature Max | Min | Rainfall | Temperature Max | Min | Rainfall | |
	C		mm	C		mm	C		mm	mm
Jan	17.8	4.6	99.9	16.9	-2.0	22.3	19.2	2.9	163.5	72.1
Feb	17.7	2.8	92.1	21.0	4.9	145.4	24.5	10.1	72.6	94.0
Mar	22.3	10.7	110.0	22.6	5.2	97.5	24.9	10.1	127.5	108.2
Apr	25.2	10.7	104.9	28.5	11.3	1.3	26.0	11.8	154.4	76.7
May	29.2	16.4	128.5	31.1	13.3	20.1	29.7	11.2	52.6	89.9
June	32.4	18.5	45.7	34.8	20.3	177.3	31.5	17.3	149.1	173.0
July	33.0	20.8	235.5	34.5	20.3	112.0	32.1	17.5	100.1	204.0
Aug	33.5	20.9	140.1	32.3	20.5	183.1	32.2	16.9	75.7	209.6
Sept	30.1	17.7	98.3	31.0	17.1	57.6	29.9	15.1	158.7	144.0
Oct	27.3	12.5	40.6	28.1	12.1	39.1	27.5	13.0	39.4	93.5
Nov	22.9	7.9	38.1	23.8	6.9	100.0	25.7	9.9	22.9	48.8
Dec	20.7	2.8	12.9	20.5	3.4	54.6	22.6	8.8	33.8	74.4

*Average precipitation for Gainesville, FL, from 1941 to 1970 (IFAS, 1981). Original data transformed to mm.

Aquic Quartzipsamments). Constituting a small part of the area,
mainly in the extremities, and surrounding the entire experimental
area is a Spodosol classified as Pomona series (sandy, siliceous,
hyperthermic, Ultic Haplaquods). Eleven composite soil samples were
taken in the experimental site in 1981 and 1982 and the results of the
analysis performed are given in Table 2. On both occasions,
magnesium, phosphorus, and potassium were at medium levels. In
agreement with the level of Ca the pH was adequate for the growth of
grasses.

Experimental Variables

The regrowth of the dwarf elephantgrass was studied under
different systems of grazing management. The grass was subjected to
the effects of different grazing pressures and lengths of grazing
cycle, each at 5 levels, as shown in Table 3. Grazing pressure was
imposed as residual leaf dry matter in kg ha^{-1} and was estimated using
a double sampling technique. Visual estimations and actual dry matter
determinations were made before and after each grazing period in order
to determine the required grazing pressure, the dry matter production,
and the stocking rate for the period (Veiga, 1983). Because residual
dry matter is subject to measurement errors, all efforts were made to
have residual leaf dry matter per ha as close as possible to the
projected values. However, fluctuations in these values were observed
throughout the grazing season. It should be indicated that a lenient
grazing pressure suggests a large amount of residual leaf left at the
end of the grazing period and conversely a high grazing pressure

Table 2. Soil fertility analysis of 11 composite samples (0 to 20 cm) taken in the experimental area in August 1981 and April 1982.

Sample no.	Pasture no.	pH 1981	pH 1982	% OM 1981	% OM 1982	Ca (ppm) 1981	Ca (ppm) 1982	Mg (ppm) 1981	Mg (ppm) 1982	P (ppm) 1981	P (ppm) 1982	K (ppm) 1981	K (ppm) 1982
1	1	6.5	6.6	1.5	1.6	608	496	56	44	36	42	28	20
2	2,3,4,5	6.7	6.6	1.8	1.8	504	68	48	44	41	24	28	
3	6	6.6	6.5	2.0	1.7	520	496	60	48	40	41	40	28
4	7,8,9	6.5	6.5	3.0	2.6	772	732	72	60	46	50	40	36
5	10	6.5	6.6	2.8	3.5	960	860	96	64	47	40	36	60
6	11,12	6.6	6.6	2.6	3.0	920	768	88	68	50	42	52	56
7	13,14,15	6.8	6.6	2.6	2.0	820	720	100	80	23	21	36	32
8	16,17,18	6.8	6.7	2.6	2.7	820	800	92	88	31	52	84	56
9	19,20,21	6.6	6.6	2.5	2.2	700	620	88	64	40	45	44	48
10	22,23,24	6.6	6.9	1.9	2.0	608	776	76	96	53	70	32	40
11	25,26	6.7	6.6	1.9	2.1	612	540	72	60	45	57	36	24
Mean		6.6	6.6	2.3	2.3	723	665	79	65	41	45	41	39

Table 3. The five levels of grazing cycles and five levels of
grazing pressure used in the experiment.

Grazing cycle§	Grazing pressure	
	Projected	Actual†
days	RLDM ha^{-1}‡	
cont.¶	500	250
14	1000	900
28	1500	1400
42	2000	2000
56	2500	2500

†Actual = Values of grazing pressure after Veiga (1983).
‡RLDM ha^{-1} = Residual leaf dry matter per ha, left after grazing.
§Grazing cycle = 2 days of grazing + days rest.
¶Cont. = Continuous grazing.

suggests a small amunt of residual leaf. Grazing cycle was expressed as number of grazing days plus number of days rest, except for the continuous treatment. Since the number of grazing days was kept constant (about 2 days), changes observed in grazing cycles were due to variation in the number of resting days. In order to accommodate the treatment combinations, the projected values and also the actual values of grazing pressures are presented in Table 3.

Experimental Design

A response surface design, namely a modified central composite non-rotatable design was used to study an incomplete 5^2 factorial of grazing cycles and grazing pressures. The central composite design consisted of three sets of points (or treatments), namely: the factorial points, the axial points, and the central point. The minimum number of treatment combinations required to conduct an experiment with two factors each at five levels, is given by the following formula: $2^k + (2k) + 1$, where k is the number of factors being studied. In this case 9 treatment combinations could be studied. In addition to these the central composite design may be modified by including four extra corner points (Littell and Mott, 1975) as shown in Fig. 1. In this experiment, all the design points shown in Fig. 1 and Table 4 were replicated twice, and the resulting 26 experimental units were distributed in a completely random manner in the field (Fig. 2). The central treatment, which would be expected to be close to the optimum combination of the experimental variables, was selected as: 28-day grazing cycle and 1500 kg of residual leaf dry matter per ha.
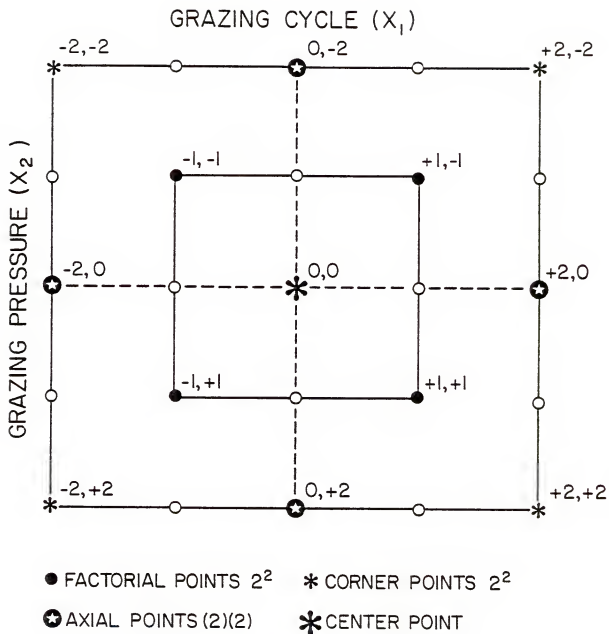
Fig. 1. Configuration of the modified central composite
non-rotatable design, including the coded treatment
combinations.

Table 4. Design points of the modified central composite non-
          rotatable design with two experimental variables, grazing
          cycle (x_1) and grazing pressure (x_2), at five levels of
          each.

Treatment no.	Category of the design points	Code x_1	x_2	Grazing cycle[†]+ (days) (x_1)	Grazing pressure (kg RLDM ha^{-1})[‡] (x_2)
1	extra	-2	-2	cont.[§]	500
2	axial	-2	0	cont.	1500
3	extra	-2	2	cont.	2500
4	factorial	-1	-1	14	1000
5	factorial	-1	1	14	2000
6	axial	0	-2	28	500
7	central	0	0	28	1500
8	axial	0	2	28	2500
9	factorial	1	-1	42	1000
10	factorial	1	1	42	2000
11	extra	2	-2	56	500
12	axial	2	0	56	1500
13	extra	2	2	56	2500

[†]Grazing cycle = rest period + 2 days of grazing.
[‡]RLDM = Residual leaf dry matter left after grazing.
[§]Cont. = Continuous grazing (0 days rest).
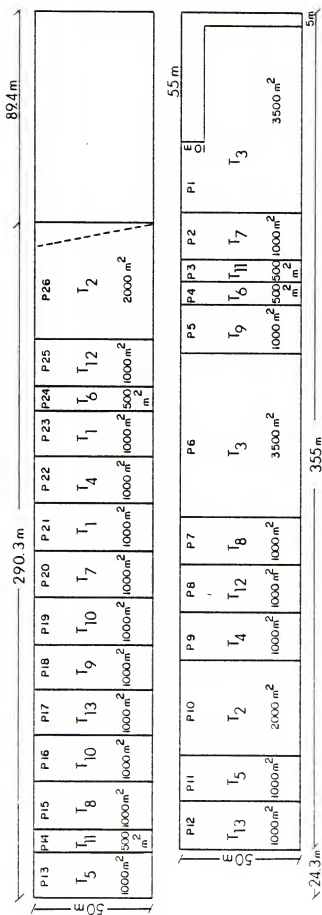
Fig. 2. Layout of the experiment and randomization of the treatments.

Physical Facilities and Size of the Experimental Pastures

The original facilities of two grazing experiments previously conducted in the same experimental area were used. Details of the construction of fences and installation of a water supply system for livestock and irrigation are given by Maraschin (1975) and Serrao (1976). In addition, an inspection and a complete clean up along the fences were done in July 1981. Wherever needed wires and posts were replaced. Extensions of the main water system were made to supply water to the east side of the experimental area. Risers were set every 10 m along the lane so that water containers were provided in all pastures, the water being controlled by a float valve.

The experimental area has a very gentle slope and was divided in two sides by a lane oriented north-south. From the area available, 3.1 ha were allocated to the experiment and then divided to accommodate 26 pastures. The following formula, presented by Maraschin (1975) and Serrao (1976) was used in order to estimate the desirable pasture size:

$$S = \frac{NdR}{DG}$$

Where S = size of pasture in m^2

            N = kg of body weight pasture^{-1} day^{-1}

            d = number of grazing days

            R = kg of leaf DM on offer kg^{-1} of body weight

            D = number of days in grazing cycle

            G = forage growth rate in kg m^{-2} day^{-1}

The calculations were based on the following assumptions:

The average weight of the animals to be used in the experiment would be 300 kg.

Each pasture would be grazed a maximum of 2 days.

The amount of dry matter on offer per 100 kg of body weight per day would be 2.0, 3.5, 5.0, 6.5, and 8.0 kg, respectively, for grazing pressures of 500, 1000, 1500, 2000, and 2500 kg of residual leaf dry matter.

The number of days in grazing cycle was expressed as the number of days rest plus number of days grazing required to attain the desired grazing pressure (except for the continuous treatment) where the cycle was considered to be 7 days.

Forage growth rates that would be achieved by the plants were estimated to be: 0.004, 0.005, 0.006, 0.004 kg m^{-2} day^{-1}, respectively, for continuous grazing, 14, 28, 42, and 56 days of grazing cycle.

It was of interest to have pasture sizes as small as possible but that would allow at least two animals grazing in a single unit during the most critical period of the year.

The size of each pasture was determined in multiples of 500 m^2 to facilitate fence construction and was always rounded off to upper limits as a measure of security. After the size and location of the experimental pastures had been established, wire gates were built and installed in each pasture.

Propagation of Dwarf Elephantgrass and Pasture Establishment

The experimental pastures were established with dwarf elephantgrass, line N-75, introduced from Dr. W. W. Hanna's nursery, located at Tifton, Georgia. In the fall of 1979, a few cuttings were brought to Florida by Dr. W. R. Ocumpaugh, and rooted in flats using vermiculite as growing medium. The flats were kept in the greenhouse until the Spring of 1980. At this time, the original plants were 60 to 80 cm in height and the onset of flowering was observed in some of them. On 28 March and 8 April, the plants were removed from the flats, their leaves eliminated, and the remaining stems divided into two or three cuttings. These stem cuttings were planted 0.5 m apart in four rows spaced 10 m apart in each section of the experimental area previously prepared. In May, over 10,000 cuttings, 5 to 10 cm long, were obtained from the established rows. They were rooted in flats containing vermiculite and were kept under shade and irrigated daily. In June, the small rooted cuttings were manually planted in 20% of the total area, in furrows 1 m apart spaced 1 m apart in the row. From 29 to 31 July, the experimental area was grazed to control weed infestation. During August, the remaining four-fifths of the area was planted using stem cuttings of 20 to 30 cm taken from the eight original rows and two small rows located in an introduction area near the experiment. About 30% of these latter cuttings were planted manually and 70% were planted mechanically using a tree planter, maintaining the spacing at 1 m x 1 m. After each planting period, sprinkler irrigation was provided to avoid water stress and to ensure the establishment of the plants. Nevertheless, death of some plants

occurred. From early to mid-September, cuttings rooted in flats were manually planted in approximately 20% of the area to replace cuttings from the previous plantings, which had died. During the establishment phase, ammonium nitrate at the rate of 25 to 30 kg N ha^{-1} was applied three times in the eight original rows, twice in the first one-fifth of the planted area and once in the remainder of the area. In order to control weeds and to create more favorable conditions to introduce a pasture legume, Roundup® (glyphosate) was sprayed between the rows of elephantgrass on 26 September. Approximately 15,000 rooted cuttings of perennial peanuts (<u>Arachis benthamii</u> Handro) were planted in early October between rows of the grass. This planting was not successful probably due to lack of soil moisture.

On 24 Apr. 1981, Butyrac-200® (2,4 DB) was applied between the rows to control the grass weed infestation, and on 28 April, the interspacings were mowed to eliminate competition from white clover (<u>Trifolium repens</u> L.) which was present over approximately 20% of the total area.

Preliminary Management of the Pastures

To gain experience with the management of the pastures and animals and also with the methodology to be used, a preliminary run of the experiment was conducted in 1981. In mid-July, over a period of about 4 days, all experimental pastures were grazed uniformly to approximately 1500 kg of residual leaf DM ha^{-1}. The pastures were then fertilized with 350 kg ha^{-1} of 10-10-10 fertilizer with 2% FTE-503. The composition of FTE-503 was the following: 3.00% B, 3.00% Cu, 18.00% Fe, 7.50% Mn, 0.20% Mo, and 7.00% Zn. The pastures were

divided using a single-wire electric fence. From 3 August to 15 October, the pastures were grazed in a manner similar to the management proposed for the 1982 experimental period. On 25 November, after a short grazing period, white clover seed at the rate of 2 kg ha^{-1} was mechanically broadcast over the experimental area. On 27 November, the pastures were fertilized with 468 kg ha^{-1} of formula 0-20-20 containing 5% sulfur and 2.5% FTE-503. At the end of the winter season, on 17 and 18 Feb. 1982, the pastures were mowed at 10 to 15 cm height in order to reduce the dead stubble and to create better conditions for the plants to regrow. A late frost occurred on 23 February, killing the initial regrowth of the dwarf elephantgrass. To stimulate spring growth, the pastures were fertilized with ammonium nitrate at the rate of 50 kg N ha^{-1} on 17 March. By this time, an infestation of tall weeds which was mainly dogfennel (Eupatorium capillifolium L.) was pulled out by hand and removed from the pastures. On 27 April, the experimental grazing period was initiated and continued until 6 Nov. 1982.

Grazing Animals and Grazing Management

A group of 30 Brown Swiss x Angus heifers, with an average weight of 320 kg at the beginning of the experiment, were maintained in two different reserve pastures of Pensacola bahiagrass. Whenever the schedule indicated, animals chosen at random were used to defoliate the experimental pastures.

The pastures were managed according to the put-and-take technique (Mott and Lucas, 1952). However, the animals were used solely to

defoliate the pastures, since the experiment was planned to study the effect of the animals on the pasture regrowth and not the effect of the pasture on the animals. Stocking rates were adjusted before each grazing period on the basis of available forage determined in terms of leaf dry matter per 100 kg of body weight. The animals were removed from the pastures when the required grazing pressure (kg of residual leaf dry matter ha^{-1}) was achieved. The technique used to quickly estimate leaf dry matter is described in detail by Veiga (1983). Each pasture was grazed in approximately 2 days, except for the continuous treatments. An adjustment of stocking rate was made when for any reason it was suspected that the required grazing pressure would not be achieved by the end of the second day of grazing. In the continuously grazed pastures it was not possible to maintain two animals at all times. Furthermore, these pastures could not be grazed with only one animal due to animal behavior problems. Thus, the nature of the continuous system was maintained by grazing these pastures as frequently as possible, so as to simulate continuous grazing.

Water was provided in all pastures and a mineral mixture was offered ad libitum in the reserve pastures. The composition of the mineral mixture was the following: Ca, not more than 24.00% and not less than 20.00%; P, not less than 10.00%, NaCl, not more than 10.00%; Fe, Cu, Co, Mn, Mg, and Zn, not less than 1.00, 0.15, 0.03, 0.25, 0.50, and 0.08%, respectively; F, not more than 0.25%; and Se, not more than 0.0015%. The animals were weighed every 28 days in order to estimate the stocking rate in terms of 100 kg liveweight ha^{-1}.

Measurements and Recordings

Tiller Population and Detailed Measurements on Individual Tillers in the Field

The number of tillers per plant was recorded before each grazing period in the rotationally grazed pastures and at each 28-day interval in the continuously grazed pastures. To characterize the dwarf elephantgrass tillers the following procedure was adopted. Two tillers with no daughter tillers were marked within each 10 plants chosen at random in each pasture. The location of the plants was marked with wood stakes numbered from one to ten and graphically located on grid paper. Suitable tillers were marked with hand made rings of plastic covered wire. The rings were pushed down as near to the soil surface as possible. The marking was done 2 days before starting the first grazing cycle in each pasture. Every effort was made to avoid disturbing the area and neighboring tillers close to the marked ones. One day before grazing, or sometimes on the same day, the following data were obtained on each marked tiller: plant height, number of basal, primary, and secondary tillers, and number of visible dead leaves. Plant height was measured as the length of the extended tiller from ground level to the ligule of the last expanded leaf. Total number of visible leaves and dead leaves were counted on each tiller. The degree of senescence was recorded by noting the presence of chlorotic or dead patches or tips on individual leaves.

Tiller Components, Leaf Area, and Morphological Measurements

Botanical separation of the parts of the grass plant into live and dead leaves, live and dead leaf sheaths, and stems was made on

samples collected before each grazing period in all pastures, except for those continuously grazed where samples were collected at 28-day intervals. For this purpose 10 tillers were sampled at random, cut to ground level, and immediately taken to the laboratory and put in a cool room. Leaf blades were separated and put in plastic bags in the refrigerator for further measurements. Leaf area was measured with a LI-COR leaf-area meter. The unit comprising the stem together with the leaf sheaths, for which the name pseudostem has been recommended (Thomas, 1980; Grant, 1981), was distinguished and its height will be referred in this study as stem height. After the stems were stripped of leaf sheaths, the following morphological characteristics were recorded: number and length of internodes, number of axillary buds, and height of the apical meristems. Percentage of apical meristems eliminated after grazing was calculated in relation to the total of tillers collected. The separated fractions were dried at 60°C for about 2 days and again weighed to the nearest gram. To accelerate the drying process, leaf sheath and stem samples were always cut with scissors into pieces 1 to 3 cm in length. Negligible amounts of dead material, mainly leaves, were found from April to July and were discarded. After early July an increased amount of dead material was observed and was processed as a separate component. The distribution of dry matter production, the relationship between the area and dry weight of leaves, i.e., the specific leaf area, and the leaf/stem ratio were calculated using the dried parts of the same 10 tillers as that used for morphological measurements. At the end of the experiment one clump was dug in each pasture to observe the size of

the root system and the presence or absence of rhizomes but no
quantitative measurements were made.

Total Nonstructural Carbohydrates

Samples to determine TNC of tiller bases were collected 1 day
before the entry of animals into the pasture and 3 days after the
removal of the animals from the pasture. Ten tillers, cut at ground
level, were taken at random in each pasture on each sampling date,
except for the continuously grazed pastures in which tillers were
collected once each 28 days. Leaves were removed in the field and the
culms immediately brought to the laboratory. Stem bases were
considered to be the first 10 cm above ground level; the remaining
aerial part of the stem was discarded. Leaf sheaths were stripped
from the stems and clean stem bases were cut into small pieces to
facilitate drying. The small portions of stem were then placed in
paper bags and exposed to a temperature of 100°C during 1 hour to
inactivate plant enzymes. After this step was completed, the samples
were dried in a forced air oven at 65°C for 72 hours. The dried stem
bases were ground in the Wiley mill using a 1 mm screen. These
samples were placed in whirl-pak plastic bags and later reground in a
UDY-Cyclone mill fitted with a 0.5 mm screen. Samples were stored in
small plastic vials for subsequent analysis. Determinations of TNC
followed the procedure developed by Christiansen (1982). Basically,
this procedure combines the enzymatic digestion method described by
Smith (1969) with the copper reduction method of Nelson (1944).
Briefly, the procedure used may be described as follows: a 0.1 g
ground sample was placed into a 25-mL Erlenmeyer flask and heated in

boiling water bath with 5 mL of distilled water to gelatinize the
starch. Five milliliters of 0.2 M acetate buffer were added in the
flask followed by 1 mL of the enzyme mixture to digest the sample.
The enzyme mixture consisted of 45 mL distilled water, 5.0 mL of 0.1
mL acetate buffer, 2.5 mL invertase concentrate, 1.25
amyloglucosidase, 0.1 g thymol. After enzyme addition, all samples
were incubated at 41°C for 48 hours, after which the contents of the
flasks were filtered into test tubes. One milliliter of an alkaline
reagent mixture was added to each tube and all tubes were placed in
boiling water for 20 min. After cooling, 1 mL of arsenomolybdate
reagent was added to each tube followed by a dilution with water to a
final volume of 10 mL. At this point, four readings of absorbance
were performed on each field sample using a Coleman JR II
spectrophotometer set at 540 nm.

Statistical Analysis

Response surface methodology was used to analyze the data
(Balaam, 1975; Littell and Mott, 1975; Mott, 1982). The estimate of
the response surface was made using the RSREG procedure for response
surface designs (SAS, 1982). The second order polynomial used was

$$y = b_0 + b_1 x_1 + b_2 x_2 + b_{11} x_1^2 + b_{22} x_2^2 + b_{12} x_1 x_2 + \epsilon$$

where y = observed response

x_1 = length of grazing cycle (days)

x_2 = grazing pressure (kg residual leaf dry matter ha^{-1})

b_0 = intercept

b_i = linear regression coefficient for x_i

b_{ii} =quadratic regression coefficient for x_i^2

b_{ij} =interaction regression coefficient

ε = random error.

With the objective of testing the fit of the model, the following analysis of variance was made (Table 5). The results of the analysis of variance were used in plotting three-dimensional response surfaces and contour graphs according to G_3D and Gcontour procedures (SAS, 1981).

Table 5. Analysis of variance.

Sources of variation	d.f.	m.s.	F
Total	25		
Regression	5		
Linear	(2)		
Quadratic	(2)		
Interaction	(1)		
Residual	20		
Lack-of-fit	(7)		
Pure error	(13)		

RESULTS AND DISCUSSION

Morphology of Dwarf Elephantgrass

The study of the morphology of dwarf elephantgrass consisted in the measurements of the following morphological characteristics: plant height, apical meristems height, stem height, number of axillary buds and internodes per tiller, and length of internodes. In addition, the percentage of apical meristems eliminated under each treatment-combination was calculated and is also discussed (Tables 6 and 7). All of these responses were well described by the fitted model. The coefficients of determination of plant height, apical meristems height, percentage of apical meristems eliminated, stem height, number of axillary buds and internodes per tiller, and length of internodes were approximately 0.98, 0.94, 0.81, 0.95, 0.88, 0.82, and 0.94, respectively (Tables 15, 16, 17, 18, 19, 20, and 21).

Plant height, measured in terms of tiller height, varied from 17.2 cm in pasture 21 (250 kg RLDM ha^{-1} and continuous grazing) to 104.1 cm in pasture 12 (2500 kg RLDM ha^{-1} and 56-day cycle). As the grazing cycle was increased and the grazing pressure was decreased the plant height was increased (Table 6 and Fig. 3). Increase in height as the plant advances in age has been reported in several tropical grasses (Tardin et al., 1971; Nascimento Jr. and Pinheiro, 1975; Gomide et al., 1979; Garcia and da Silva, 1980), including tall varieties of elephantgrass (Vieira and Gomide, 1968; Pedreira and Boin, 1969; Andrade and Gomide, 1971).

Table 6. Plant height, apical meristems height, and percentage of
          elimination of apical meristems in dwarf elephantgrass.

Pasture no.	Treatment combinations		Plant height	Apical meristems height	Apical meristems elimination
	Estimated grazing pressure	Grazing Cycle†			
	kg RLDM ha^{-1}‡	days	cm	cm	%
21	250	cont.§	17.2	7.8	65.0
23	250	cont.	21.7	8.1	73.3
10	1400	cont.	44.8	16.5	45.0
26	1400	cont.	44.8	16.9	44.0
1	2500	cont.	66.8	24.4	50.0
6	2500	cont.	67.9	26.4	57.5
9	900	14	45.5	12.2	50.8
22	900	14	46.5	13.8	47.7
11	2000	14	67.6	19.0	49.1
13	2000	14	69.3	12.1	43.6
4	250	28	49.4	9.4	56.7
24	250	28	49.6	11.0	51.7
2	1400	28	71.5	17.9	50.0
20	1400	28	69.3	17.8	41.7
7	2500	28	87.6	24.6	48.0
15	2500	28	82.7	24.2	52.0
5	900	42	75.0	14.2	32.5
18	900	42	78.4	16.6	42.5
16	2000	42	85.9	25.1	30.0
19	2000	42	85.2	22.9	42.5
3	250	56	71.2	11.7	46.7
14	250	56	71.2	17.8	50.0
8	1400	56	93.1	23.8	26.7
25	1400	56	82.8	22.7	35.0
12	2500	56	104.1	24.9	25.0
17	2500	56	90.3	29.7	35.0

†Grazing cycle = Rest period + 2 days grazing period.
‡RLDM = Residual leaf dry matter left after grazing.
§Cont. = Continuous grazing.

Table 7. Morphological characteristics of dwarf elephantgrass tillers, before each grazing cycle.

Pasture no.	Treatment combinations Estimated grazing pressure	Grazing cycle†	Stem height	Number of axillary buds per tiller	Number of internodes per tiller	Length of internodes
	kg RLDM‡ ha⁻¹	days	cm			cm
21	250	cont.§	13.8	6.4	12.6	0.7
23	250	cont.	13.7	7.2	13.9	0.6
10	1400	cont.	26.0	10.2	15.5	1.1
26	1400	cont.	28.3	11.1	15.2	1.1
1	2500	cont.	35.4	14.5	18.4	1.3
6	2500	cont.	37.5	15.2	19.5	1.4
9	900	14	21.7	8.1	12.8	1.0
22	900	14	22.9	9.1	14.9	1.0
11	2000	14	29.4	11.0	16.7	1.2
13	2000	14	34.0	12.9	17.8	1.3
4	250	28	17.7	6.2	12.5	0.8
24	250	28	19.5	8.4	13.7	0.8
2	250	28	28.2	12.0	16.0	1.1
20	1400	28	28.1	10.9	16.0	1.1
7	2500	28	35.3	14.7	19.0	1.3
15	2500	28	36.6	13.3	17.2	1.4
5	900	42	25.3	9.9	14.4	0.9
18	900	42	27.5	9.9	15.0	1.1
16	2000	42	37.0	15.2	19.8	1.1
19	2000	42	33.7	12.8	17.5	1.3
3	250	56	21.4	7.9	12.3	1.0
14	250	56	28.4	11.0	14.8	1.2
8	1400	56	34.8	23.5	16.5	1.4
25	1400	56	33.2	14.0	17.5	1.3
12	2500	56	36.7	13.7	16.8	1.5
17	2500	56	41.4	14.4	19.4	1.5

†Grazing cycle = Rest period + 2 days grazing period.
‡RLDM = Residual leaf dry matter left after grazing.
§Cont. = Continuous grazing.

Fig. 3. Contour map of plant height of dwarf elephantgrass as affected by length of grazing cycle and grazing pressure, 1982. (R^2 = 0.98, CV = 5.24%)

An analysis of Table 6 and Fig. 4 indicates that the apical meristems were relatively low at high grazing pressures and short grazing cycles and increased in height as the grazing pressure decreased and the grazing cycle increased. The response is similar to that of plant height suggesting that the grass tends to change its form under different grazing conditions. The data in Table 6 also suggest that grazing pressure had the greatest effect upon the elimination of apical meristems. The percentage of apical meristems eliminated varied from 25.0% in pasture 12 (2500 kg RLDM ha^{-1} and 56-day cycle) to 73.3% in pasture 33 (250 kg RLDM ha^{-1} and continuous grazing). It should be mentioned that at the beginning of the growing period the apical meristems were close to the ground in all pastures. However, the apices of some stems were grazed in pastures subjected to heavier grazing pressure (250 kg RLDM ha^{-1}). On the other hand, in the second half of the experimental period, after about 1 August, lower stocking rates were required to attain the projected grazing pressure which may have reduced the number of apical meristems removed at heavy grazing pressures and short grazing cycles. In fact, the use of high stocking rates or the maintenance of animals in the continuously grazed pastures resulted in the elimination of a large number of apical meristems. It has been suggested by several authors that the position of the growing points at the time of defoliation is an important morphological factor in determining the persistence of forage grasses (Booysen et al., 1963; Jewiss, 1966; Langer, 1972; Youngner, 1972; Dahl and Hyder, 1977; Gomide et al., 1979; Dovrat et al., 1980; Humphreys, 1981). Indeed, regrowth of tropical grasses is

Fig. 4. Contour map of height of apical meristems of dwarf
elephantgrass as affected by length of grazing cycle
and grazing pressure, 1982. (R^2 = 0.94, CV = 9.16%)

associated with the fate of apical meristems following defoliation
(Andrade and Gomide, 1971; Tardin et al., 1971; Nascimento Jr. and
Pinheiro, 1975; Gomide et al., 1979; Dovrat et al., 1980). Andrade
and Gomide (1971) observed that a rapid and early elongation of
internodes in elephantgrass resulted in the elimination of a higher
number of apical meristems. Stem growth, promoted by stem elongation,
increases apical meristems vulnerability to defoliation (Branson,
1953; Booysen et al., 1963; Gomide, 1973; Ludlow, 1976; Dahl and
Hyder, 1977; Gomide et al., 1979; Humphreys, 1981). In the Andrade
and Gomide (1971) trial all apical meristems were eliminated when the
plants were cut at 56 days of age. Cutting each 28 days allowed the
survival of apical meristems which in turn engendered good regrowth.
Muldoon and Pearson (1979b) reported that the initial regrowth of
hybrid _Pennisetum_ was delayed when the apical meristems were
decapitated. When the apical meristems were left intact, a more rapid
initial regrowth was observed.

The data presented in Table 7 and the contours of equal response
(Figs. 5, 6, 7, and 8) indicate clearly that the combined effect of
grazing pressure and grazing cycle caused marked changes in the
morphology of dwarf elephantgrass. Stem height ranged from 13.7 cm in
pasture 23 (250 kg RLDM ha^{-1} and continuous grazing) to 41.4 cm in
pasture 17 (2500 kg RLDM ha^{-1} and 56-day cycle). Figure 5 suggests
that stem height was increased as the grazing cycle was increased and
the grazing pressure was decreased. At high grazing pressures stem
height was greatly reduced (Table 7 and Fig. 5). A quadratic effect
of grazing cycle and the interaction of grazing pressure and grazing
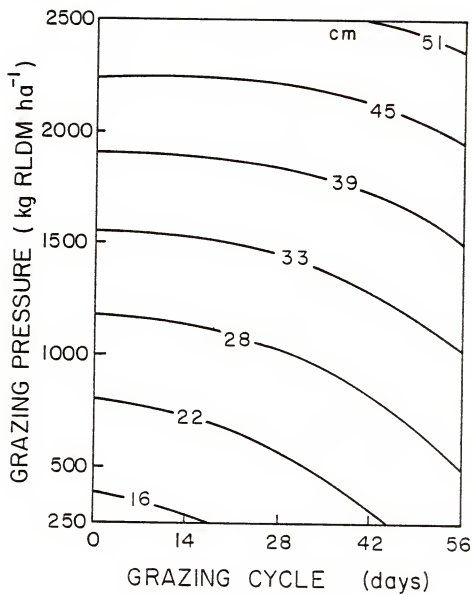
Fig. 5. Contour map of stem height of dwarf elephantgrass as influenced by length of grazing cycle and grazing pressure, 1982. (R^2 = 0.95, CV = 6.41%)
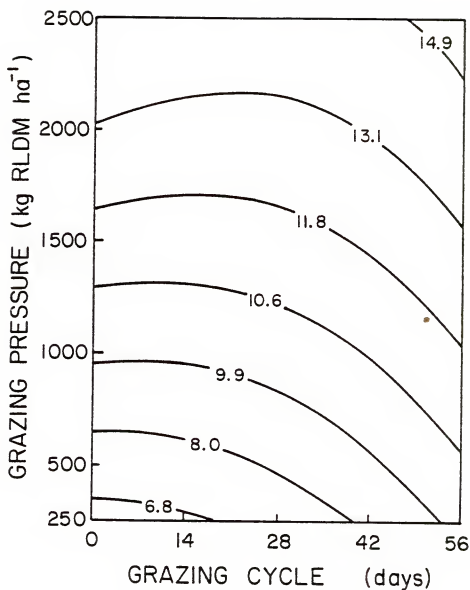
Fig. 6.   Contour map of number of axillary buds per tiller of
          dwarf elephantgrass as affected by length of grazing
          cycle and grazing pressure, 1982.   (R^2 = 0.88, CV = 9.36%)
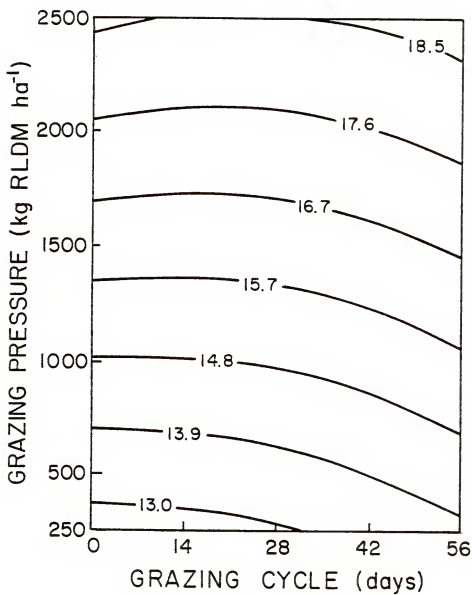
Fig. 7. Contour map of number of internodes per tiller of
dwarf elephantgrass as affected by length of grazing
cycle and grazing pressure, 1982. ($R^2 = 0.82$, CV = 6.80%)
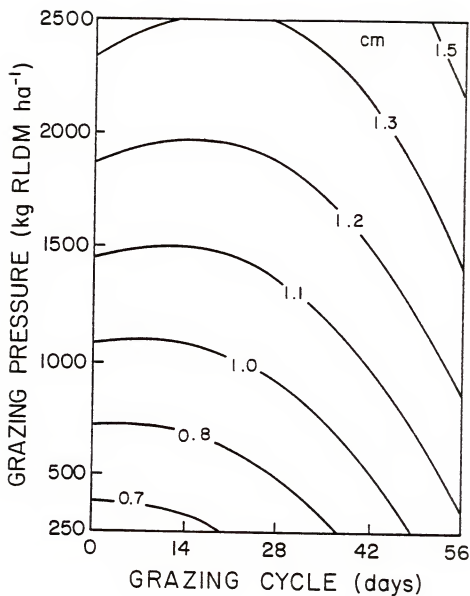
Fig. 8. Contour map of length of internodes of dwarf elephant-grass as affected by length of grazing cycle and grazing pressure, 1982. (R^2 = 0.94, CV = 5.78%)

cycle is also suggested. Stems were smaller at high grazing pressures and short grazing cycles. However, even under continuous grazing, stem growth occurred when the plants were subjected to a more lenient grazing pressure.

The number of axillary buds per tiller was influenced by the same conditions which affected stem growth. High grazing pressures, independently of grazing cycle, depressed the number of axillary buds per tiller (Table 7 and Fig. 6). An examination of Table 7 and Figs. 5 and 6 suggests that the appearance of axillary buds was associated with the growth of well developed stems. The interaction of grazing pressure and grazing cycle is also suggested since the effect of high grazing pressures is to increase the number of axillary buds at long grazing cycles and low grazing pressures appear to compensate for the effect of short grazing cycles.

The number of internodes per tiller of dwarf elephantgrass varied from 12.3 to 19.8. Greater numbers of internodes were observed at low grazing pressures in all grazing cycles (Table 7 and Fig. 7). Although Fig. 7 suggest an increase in the number of internodes as grazing pressure is decreased and grazing cycle is increased, the low variation in number of internodes (Tables 7 and 20) supports the idea that the number of internodes is genetically established and inherent to each genotype. Because only visible internodes were counted it is possible that greater elimination of apical meristems at higher grazing pressures prevented the full expression of this morphological characteristic.

Cultivars of elephantgrass differ in many morphological characteristics (Bogdan, 1977; Muldoon and Pearson, 1979c). However,

there is no doubt that differences in height between tall and dwarf
varieties of elephantgrass is due to the length of internodes. The
pattern of internode elongation is due to differentiation of cells of
apical meristems. Furthermore, elongation of internodes increases
plant height, reduces the density of buds close to the ground, changes
canopy structure, reduces the number of growing points that remain
after defoliation, and may also be associated with a decline in
nutritive value (Branson, 1953; Booysen et al., 1963; Jewiss, 1966;
Langer, 1972; Gomide, 1973; Ludlow, 1976; Dahl and Hyder, 1977; Gomide
et al., 1979; Dovrat et al., 1980; Humphreys, 1981). In this
research, the most interesting response of dwarf elephantgrass was the
reduction of the elongation rate of internodes at high grazing
pressures and short grazing cycles. By maintaining shorter internodes
and assuming a more prostrate growth habit the grass quickly adapted
itself to frequent and intense defoliation. Although this phenotypic
adaptation was clearly evident in plants subjected to continuous
grazing and the highest grazing pressure (250 kg RLDM ha^{-1}), it was
also observed at high grazing pressures in combination with grazing
cycles of 14 and 28 days (Table 7 and Fig. 8). This morphological
response prevented the removal of some apical meristems which in turn
may have allowed herbage production to continue throughout the grazing
season. Figure 8 also suggests that as the grazing pressure was
decreased and the grazing cycle was increased, the length of
internodes was increased. Another interesting fact is that elongation
of internodes was not affected by the length of grazing cycle when the
plants were subjected to lower grazing pressures (2500 kg RLDM ha^{-1}).

Tillering of Dwarf Elephantgrass

Tillering of dwarf elephantgrass was observed throughout the growing season in marked plants and tillers. The number of main tillers per plant and number of basal, primary and secondary tillers per main tiller were recorded (Table 8).

The coefficients of determination of number of main tillers per plant and number of basal, primary and secondary tillers per main tiller were 0.60, 0.74, 0.37, and 0.42, respectively (Tables 22, 23, 24, and 25). The linear components of the model explained 52, 62, 16, and 22% of the total variation for number of tillers per plant and number of basal, primary, and secondary tillers per main tiller, respectively. The quadratic and interaction terms accounted for 1, and 7, 10 and 2, 2 and 20, and 20 and 0% of the variability, respectively.

An analysis of Table 8 and Figs. 9 and 10 indicates a decrease in the number of main tillers per plant as the grazing cycle was shortened and the grazing pressure was increased. The number of main tillers per plant varied from 15.4 in pasture 21 (250 kg RLDM ha^{-1} and continuous grazing) to 34.9 in pasture 12 (2500 kg RLDM ha^{-1} and 56-day cycle). At short grazing cycles, a tendency of the number of main tillers per plant to increase under more lenient grazing pressures suggests an interaction between grazing cycle and grazing pressure. In tropical grasses the number of tillers per plant is usually low when compared with temperate species (Langer, 1963, 1972; Jewiss, 1966, 1972; Pedreira, 1975; Bogdan, 1977; Muldoon and Pearson, 1979c; Mott, 1983). The number of main tillers per plant found in this research is in agreement with the low number of tillers found by

Table 8. Tillering of dwarf elephantgrass.

Pasture no.	Estimated grazing pressure	Grazing Cycle†	Number of main tillers per plant	basal	primary	secondary
	kg RLDM ha^{-1}‡	days				
21	250	cont.§	15.4	0.65	3.58	0.17
23	250	cont.	15.7	0.50	3.55	0.17
10	1400	cont.	28.0	0.20	2.74	0.06
26	1400	cont.	24.2	0.08	2.24	0.10
1	2500	cont.	24.6	0.10	2.14	0.08
6	2500	cont.	25.7	0.13	2.70	0.00
9	900	14	21.7	0.25	2.58	0.07
22	900	14	20.4	0.12	3.08	0.11
11	2000	14	32.4	0.20	2.92	0.18
13	2000	14	30.4	0.14	2.93	0.09
4	250	28	22.4	0.37	2.92	0.18
24	250	28	22.8	0.25	3.15	0.68
2	1400	28	18.3	0.10	2.33	0.12
20	1400	28	23.1	0.15	2.90	0.10
7	2500	28	26.0	0.08	3.08	0.10
15	2500	28	34.4	0.10	2.00	0.06
5	900	42	22.9	0.25	2.10	0.00
18	900	42	25.0	0.28	3.28	0.13
16	2000	42	31.3	0.17	2.83	0.10
19	2000	42	26.5	0.08	2.45	0.15
3	250	56	27.6	0.27	2.10	0.10
14	250	56	32.9	0.43	2.33	0.20
8	1400	56	32.0	0.17	2.33	0.03
25	1400	56	28.9	0.25	3.05	0.05
12	2500	56	34.9	0.05	2.20	0.00
17	2500	56	27.3	0.10	3.00	0.05

†Grazing cycle = Rest period + 2 days grazing period.
‡RLDM = Residual leaf dry matter left after grazing.
§Cont. = Continuous grazing.
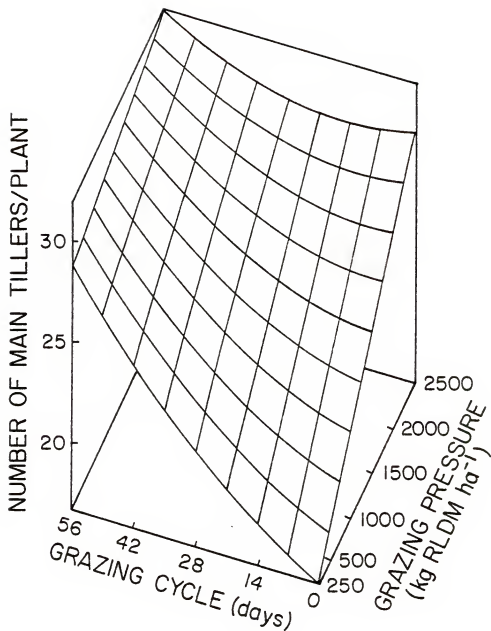
Fig. 9. Response surface of the effect of grazing cycle and grazing pressure upon the number of main tillers per plant of dwarf elephantgrass, 1982. ($R^2 = 0.60$, CV = 14.54%)
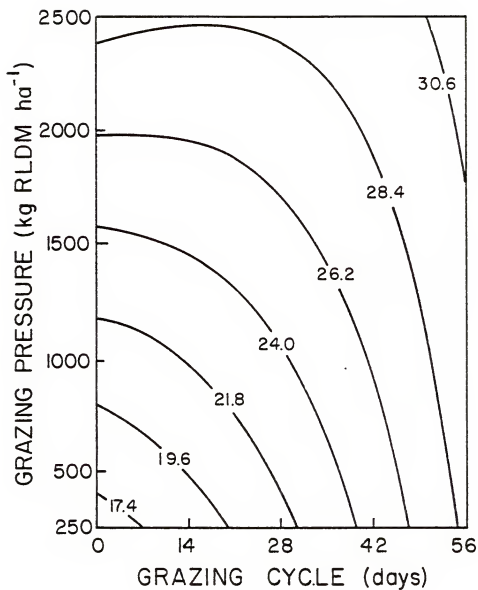
Fig. 10. Contour map of number of main tillers per plant of dwarf elephantgrass as affected by length of grazing cycle and grazing pressure, 1982. ($R^2 = 0.60$, CV = 14.54%)

Boddorff (1982) in dwarf elephantgrass and in interspecific hybrids of
Pennisetum americanum x P. purpureum.

In contrast to the number of main tillers per plant, the number
of basal tillers per tiller increased as the grazing cycle was
shortened and the grazing pressure was increased (Fig. 11). A
quadratic effect of grazing pressure is also suggested. The number of
basal tillers per main tiller varied from 0.05 in pasture 12 (2500 kg
RLDM ha^{-1} and 56-day cycle) to 0.65 in pasture 21 (250 kg RLDM ha^{-1}
and continuous grazing). The reduction in the length of internodes,
as already discussed, and a higher production of basal tillers
resulted in plants with a more prostrate growth habit. It should be
emphasized that this morphological reaction is a clear evidence of the
capacity of the grass to adapt itself to stress conditions. In the
pasture environment tillering may be significantly affected by
grazing. According to Youngner (1972) when stem apices are removed,
apical dominance is broken and the rate of tiller production is
increased by activation of basal and lateral buds. Defoliation may
enhance tillering, even when apices remained undamaged, by creating a
more favorable light environment which would be expected to stimulate
the growth and activation of buds (Jewiss, 1972; Laude, 1972;
Youngner, 1972).

The number of primary tillers per tiller of dwarf elephantgrass
affected by grazing pressure and grazing cycle is recorded in Table 8
and Fig. 12. A greater number of primary tillers were observed at
high grazing pressures and short grazing cycles. However, at longer
grazing cycles the number of primary tillers tended to increase as the
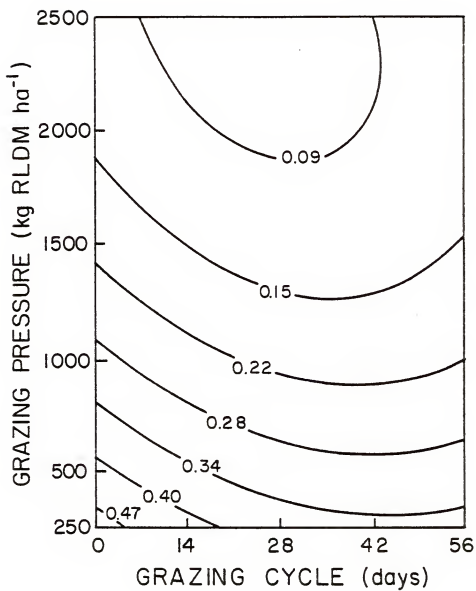
Fig. 11. Contour map of number of basal tillers per tiller
          of dwarf elephantgrass as affected by length of
          grazing cycle and grazing pressure, 1982. ($R^2 = 0.74$,
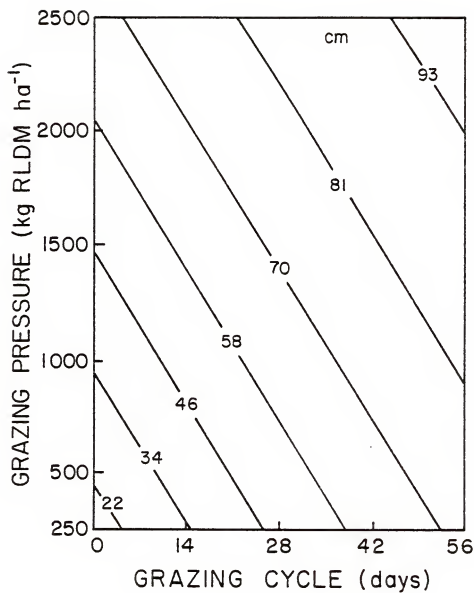   CV = 39.25%)
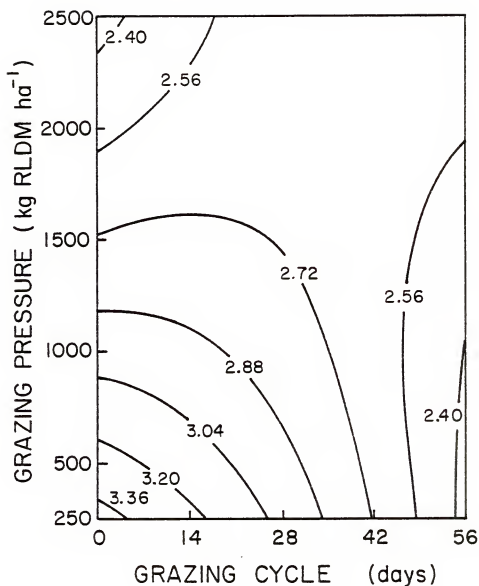
Fig. 12. Contour map of primary tillers per tiller of dwarf
          elephantgrass as affected by length of grazing cycle
          and grazing pressure, 1982. (R^2 = 0.38, CV = 14.82%)

grazing pressure was decreased. This change in the effect of grazing
pressure with grazing cycle is an indication of a grazing cycle-
grazing pressure interaction, (Fig. 12). From the overall means and
as shown in Tables 8, 23, 24, and 25 and Figs. 11, 12, and 13, it can
be concluded that primary tillers constitute the predominant form of
tillering in dwarf elephantgrass under a wide range of management
systems. Indeed, a greater number of primary tillers were found in
all pastures in comparison to basal tillers. This tillering response
is supported by the research of Belyuchenko (1980) who observed that
the proportion of new tillers in the regrowth of elephantgrass is
modified by the height of cutting. When plants were cut at 10 or 15
cm, tillers originated from basal buds of the crown. Cuts at 15 cm or
higher produced a higher number of aerial tillers arising from
axillary buds.

The presence of primary tillers in all treatment combinations,
even in those with low percentage of apical meristems eliminated,
should be considered as an indication of tillering ability of dwarf
elephantgrass and as a measure of its efficiency as a forage producer.

Secondary tillers were absent or appeared at a low rate in
pastures subjected to low grazing pressures (Table 8). On the other
hand, independent of the grazing cycle, high grazing pressure (250 kg
RLDM ha^{-1}) stimulated the appearance of secondary tillers (Table 8 and
Fig. 13). A quadratic effect of grazing pressure in reducing the
number of secondary tillers is more apparent under continuous grazing
and a 56-day cycle. Increased shading, due to the development of
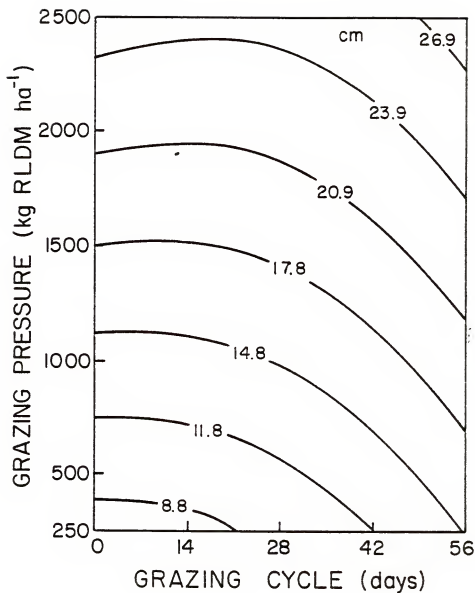greater canopy closures, and low elimination of apical meristems
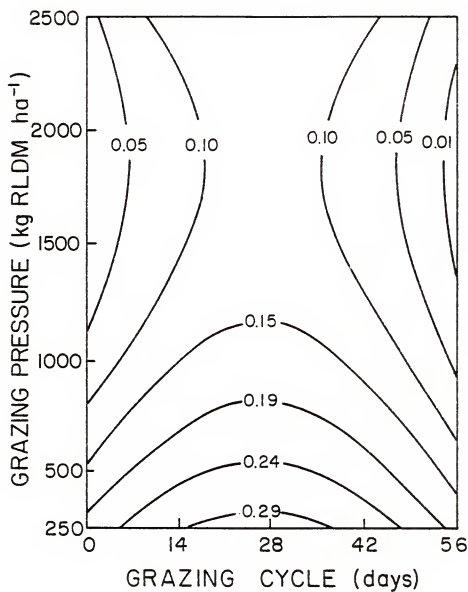
Fig. 13. Contour map of secondary tillers per tiller of dwarf
elephantgrass as affected by length of grazing cycle
and grazing pressure, 1982. (R^2 = 0.42, CV = 92.27%)

may have induced bud inhibition at low grazing pressures and long
grazing cycles (Langer, 1963; Laude, 1972; Youngner, 1972; Dahl and
Hyder, 1977).

Dry Matter Distribution in Tillers of Dwarf Elephantgrass

Dry matter (DM) distribution in tillers of elephantgrass as
affected by grazing pressure and length of grazing cycle is shown in
Table 9. The total DM produced over the whole season as well as the
distribution of this DM in leaf blades, leaf sheaths, and stems is
given in g DM per 10 tillers. The total DM produced per 10 tillers
varied from 51.3 and 53.2 g in pastures 23 and 21, respectively (250
kg RLDM ha^{-1} and continuous grazing) to 339.0 and 374.5 g in pastures
12 and 17, respectively (2500 kg RLDM ha^{-1} and 56-day cycle).

The linear components of the model explained approximately 95% of
the total variation while the quadratic and interaction terms
accounted for about 1, and 0%, respectively (Table 26).

Dry matter production in tillers was increased by reducing the
grazing pressure and increasing the length of the grazing cycle (Table
9 and Fig. 14). The shape of the response surface (Fig. 15) suggests
that the rate of increase in the total dry matter produced per 10
tillers was progressively increased as grazing pressure was decreased
and grazing cycle was increased. From Table 9 it can be calculated
that tillers of plants subjected to low grazing pressure and long
grazing cycles (2000 and 2500 kg RLDM ha^{-1} and 42- and 56-day cycles,
respectively) were producing approximately 6 to 7 times the dry matter
when compared with tillers subjected to continuous grazing and high

Table 9. Distribution of dry matter production in dwarf elephantgrass tillers.

| Pasture no. | Treatment combinations | | Distribution of dry matter | | | |
	Estimated grazing pressure	Grazing Cycle†	leaf blade	leaf sheath	stem	total
	kg RLDM ha⁻¹‡	days	———— g DM 10 tillers⁻¹ ————			
21	250	cont.§	18.3	17.3	17.5	53.2
23	250	cont.	16.3	17.2	17.8	51.3
10	1400	cont.	73.5	48.7	50.3	172.5
26	1400	cont.	75.4	56.0	61.2	192.6
1	2500	cont.	100.2	57.8	77.0	235.0
6	2500	cont.	115.0	65.8	83.3	264.0
9	900	14	57.5	34.3	41.0	132.8
22	900	14	69.0	47.1	49.1	115.2
11	2000	14	93.7	56.7	59.4	209.8
13	2000	14	93.4	51.4	62.6	207.4
4	250	28	48.3	29.2	33.0	110.5
24	250	28	56.3	43.0	49.5	148.8
2	1400	28	92.8	57.3	65.8	216.0
20	1400	28	103.7	64.5	75.7	243.8
7	2500	28	136.4	72.6	96.8	305.8
15	2500	28	128.2	55.0	90.2	273.4
5	900	42	90.8	49.8	66.8	207.3
18	900	42	106.5	58.3	59.8	224.5
16	2000	42	122.7	69.0	95.7	287.3
19	2000	42	148.0	73.3	86.5	307.8
3	250	56	78.7	37.0	43.0	158.7
14	250	56	81.7	45.3	54.0	181.0
8	1400	56	141.0	62.7	95.0	298.7
25	1400	56	139.0	62.5	89.5	291.0
12	2500	56	160.5	70.5	108.0	339.0
17	2500	56	183.5	76.0	115.0	374.5

†Grazing cycle = Rest period + 2 days grazing period.
‡RLDM = Residual leaf dry matter left after grazing.
§Cont. = Continuous grazing.
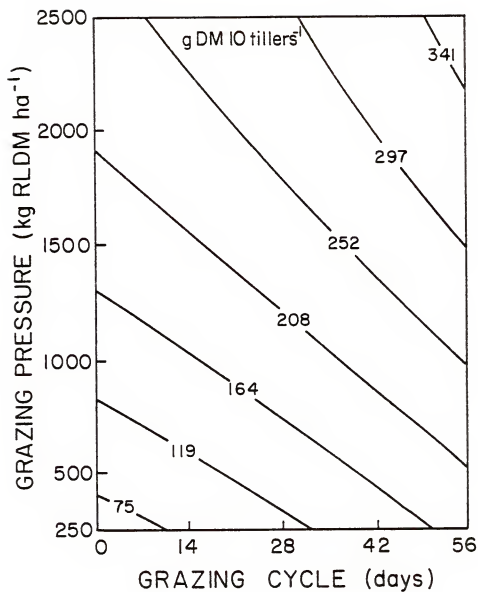
Fig. 14. Contour map of total dry matter in tillers of dwarf elephantgrass as affected by length of grazing cycle and grazing pressure, 1982. (R^2 = 0.96, CV = 8.75%)

Fig. 15. Response surface of the effect of length of grazing
cycle and grazing pressure upon total dry matter
produced per 10 tillers of dwarf elephantgrass,
1982. (R^2 = 0.96, CV = 8.75%)

grazing pressure (250 kg RLDM ha^{-1}). The magnitude of the response is
even higher if we consider that in the highest grazing pressure and
short grazing cycle (250 kg RLDM ha^{-1} and continuous grazing) the
number of main tillers per plant was drastically reduced. There is no
doubt that the decrease in DM produced per tiller under intensive
grazing was due to the effects of short grazing cycles and high
grazing pressures. Therefore, it should be expected that survival of
the plants or number of tillers per plant may have affected the DM
produced per tiller. From surveys conducted at the beginning and end
of the experimental period it was determined that the population
density was about 7500 plants ha^{-1} and the survival of plants was 100%
regardless of treatment. It was also observed that the basal area of
plants subjected to continuous grazing and higher grazing pressure
(250 kg RLDM ha^{-1}) was drastically reduced, whereas in pastures
subjected to low grazing pressures and long grazing cycles the basal
area of the clumps increased. Reductions and increases in the area
occupied by the plants may be explained by changes in number and size
of main tillers per plant as well as by the variation in number of
basal and primary tillers per tiller. Furthermore, changes in canopy
structure and size of the plants may have affected the competition for
light, water, and nutrients, between tillers within plants, and hence
the dry matter produced per tiller as indicated by Donald (1963) and
Rhodes and Stern (1978).

The effect of the experimental variables upon leaf blade, leaf
sheath, and stem DM produced per 10 tillers was similar to that of
total dry matter per 10 tillers (Table 9 and Figs. 16, 17, and 18).
Average values of leaf blade and leaf sheath DM per 10 tillers varied
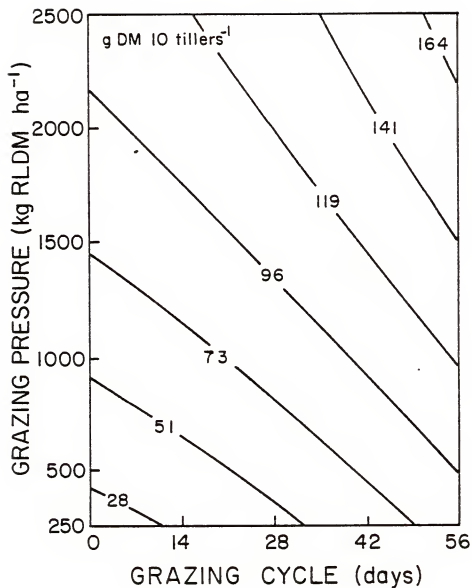
Fig. 16. Contour map of dry matter production of leaf blades
          in tillers of dwarf elephantgrass as affected by
          length of grazing cycle and grazing pressure, 1982.
          (R^2 = 0.97, CV = 8.65%)
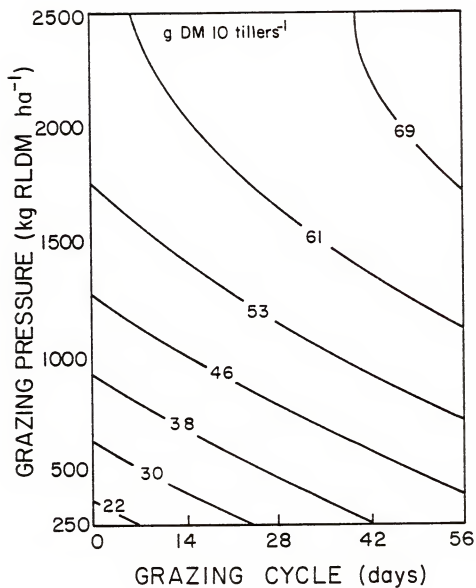
Fig. 17. Contour map of dry matter production of leaf sheaths
in tillers of dwarf elephantgrass as affected by
length of grazing cycle and grazing pressure, 1982.
(R^2 = 0.88, CV = 11.93%)
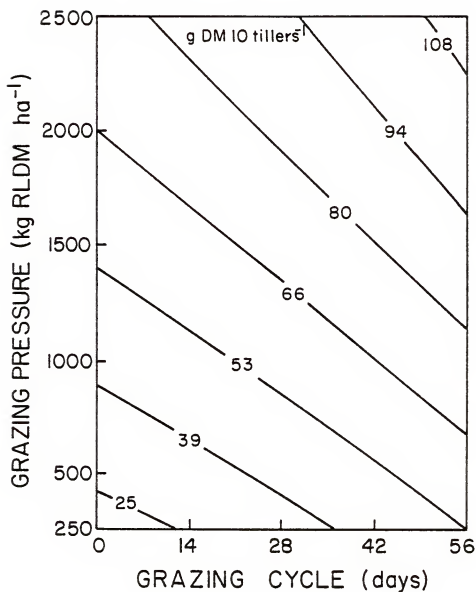
Fig. 18. Contour map of dry matter production of stems in
          tillers of dwarf elephantgrass as affected by
          length of grazing cycle and grazing pressure, 1982.
          (R^2 = 0.94, CV = 10.96%)

from 16.3 and 17.2 g in pasture 23 (250 kg RLDM ha^{-1} and continuous grazing) to 183.5 and 76.0 g in pasture 17 (2500 kg RLDM ha^{-1} and 56-day cycle), respectively. The DM of stems ranged from 17.5 g in pasture 21 (250 kg RLDM ha^{-1} and continuous grazing) to 115.0 g in pasture 17 (2500 kg RLDM ha^{-1} and 56-day cycle). The second degree model accounted for approximately 97, 88, and 94% of the total variation for leaf blade, leaf sheath, and stem DM produced per 10 tillers, respectively (Tables 27, 28, and 29). The linear components of the model explained 96, 81, and 93% of the total variation, while the quadratic and interaction terms accounted for only 1 and 0, 6 and, and 1 and 0%, respectively.

Favorable conditions for high DM production of leaf blades, leaf sheaths, and stems were met at low grazing pressures in combination with long grazing cycles (Figs. 16, 17, and 18).

From Table 9 it is easily perceived that most of the DM produced was allocated to the leaf components of the tiller, i.e., leaf blade and leaf sheath. In addition, the proportion of these components was also changed as the grazing pressure was decreased and the grazing cycle was increased. Figure 17 suggests that leaf sheath growth is stimulated under lower grazing pressures. Dry matter production of stems was reduced by high grazing pressure, even under conditions where the stems had more time to elongate (Table 9 and Fig. 18).

In this experiment, grazing pressure levels were imposed on the basis of residual leaf blade DM and therefore the increase in DM produced in different parts of the tillers as the grazing pressure is decreased and the grazing cycle is increased may be related to the

interaction of several factors including: the residual leaf area left after each grazing period, fluctuations in carbohydrate reserves, and morphological changes of the plants as well as a greater elimination of apical meristems under high grazing pressures. The response observed is consistent with the increase in growth rate of this grass as reported by Veiga (1983). Since total DM production consists of the contribution of individual tillers these results are supported by results from cutting experiments (Werner et al., 1965/1966; Vieira and Gomide, 1968; Andrade and Gomide, 1971), and grazing trials where conditions of low grazing pressures and long rest periods after each defoliation resulted in increased forage DM production (Maraschin, 1975; Serrao, 1976; Santillan, 1983).

Leaf/Stem Ratio of Dwarf Elephantgrass

The separation of tiller components in leaf blades, leaf sheaths, and stems allowed the calculation of the following leaf/stem ratios: leaf blade/(leaf sheath + stem) and (leaf blade + leaf sheath)/stem (Table 10). The analyses of variance are presented in Tables 30 and 31, respectively. The coefficients of determination indicate that the variation in leaf blade/(leaf sheath + stem) ratio can be explained by the fitted model ($R^2 = 0.73$) whereas the variation in (leaf blade + leaf sheath)/stem ratio was not well described by the second order model ($R^2 = 0.26$). The linear components of the model explained 65 and 14% of the total variation for leaf blade/(leaf sheath + stem) and (leaf blade + leaf sheath)/stem ratios, respectively. The quadratic and interaction terms accounted for about 1 and 7, and 11 and 1% of the variability, respectively.

Table 10. Dwarf elephantgrass leaf blade/stem ratio, (leaf blade + leaf sheath)/stem ratio, and leaf blade/(leaf sheath + stem) ratio.

Pasture no.	Estimated grazing pressure	Grazing Cycle†	(L + LS)/S ratio	L/(LS +S)¶ ratio
		Treatment combinations	Dwarf elephantgrass	
	kg RLDM ha⁻¹‡	days		
21	250	cont.§	2.44	0.54
23	250	cont.	2.30	0.48
10	1400	cont.	2.89	0.78
26	1400	cont.	2.26	0.66
1	2500	cont.	2.35	0.80
6	2500	cont.	2.26	0.79
9	900	14	2.97	0.83
22	900	14	2.67	0.77
11	2000	14	2.89	0.85
13	2500	14	2.53	0.85
4	250	28	2.65	0.79
24	250	28	2.52	0.68
2	1400	28	2.57	0.79
20	1400	28	2.38	0.78
7	2500	28	2.20	0.81
15	2500	28	2.15	0.91
5	900	42	2.52	0.85
18	900	42	2.84	0.91
16	2000	42	2.04	0.75
19	2000	42	2.68	0.96
3	250	56	2.73	1.01
14	250	56	2.29	0.80
8	1400	56	2.22	0.90
25	1400	56	2.29	0.92
12	2500	56	2.34	0.93
17	2500	56	2.38	1.00

†Grazing cycle = Rest period + 2 days grazing period.
‡RLDM = Residual leaf dry matter left after grazing.
§Cont. = Continuous grazing.
¶L = Leaf blade, LS = Leaf sheath, S = Stem.

The leaf blade/(leaf sheath + stem) ratio varied from 0.48 in
pasture 23 (250 kg RLDM ha^{-1}) and continuous grazing) to 1.01 in
pasture 3 (250 kg RLDM ha^{-1} and 56-day cycle). Figure 19 indicates
that as grazing pressure was decreased and the grazing cycle was
increased the leaf blade/(leaf sheath + stem) ratio tends to increase.
However, it should be noted that higher ratios were recorded at lower
and higher grazing pressures in combination with longer grazing
cycles, whereas lower ratios resulted from high grazing pressures and
short grazing cycles; suggesting an interaction of grazing pressure
with grazing cycle (Table 10 and Fig. 19). Similar responses have
been reported in tall varieties of elephantgrass by Pedreira and Boin
(1969) and Velez-Santiago and Arroyo-Aguilu (1981). The overall mean
of leaf blade/(leaf sheath + stem) ratio (0.81) (Table 30) is lower
than that reported by Veiga (1983) and may be related to differences
in sampling procedures. It should be expected that grazing cycles
longer than 56 days would cause a decrease in leaf blade/(leaf sheath
+ stem) ratio due to an increase in leaf sheath growth and stem
elongation.

It is well know that leaf and stem tissues of grasses differ in
nutritive value. Few attempts have been made to characterize the
amounts and quality of leaf sheaths which make up, in some tropical
grasses, a large proportion of the forage dry matter produced. In
fact, leaf blades have the highest nutritive value for the animal and
the leaf blade/(leaf sheath + stem) ratio usually gives an indication
of the potential quality of the forage (Veiga, 1983). In addition,
when the proportion of leaf blades allows a high degree of
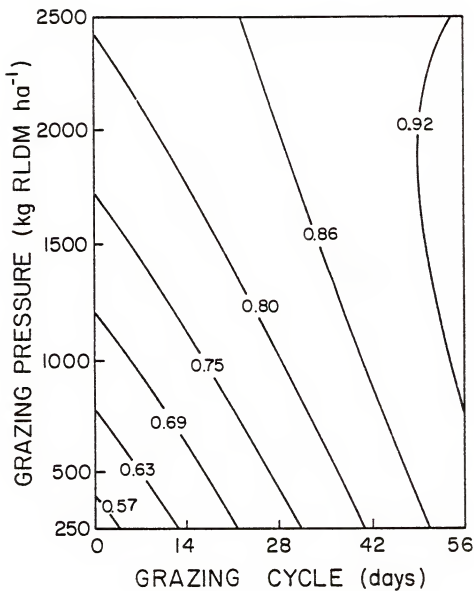
Fig. 19. Contour map of leaf blade/(leaf sheath + stem) ratio of dwarf elephantgrass as affected by length of grazing cycle and grazing pressure, 1982. ($R^2 = 0.73$, CV = 8.98%)

selectivity, a higher animal performance has been achieved (Chacon et al., 1978). On the other hand, the calculation of (leaf blade + leaf sheath)/stem ratio would give a better idea of the partitioning of assimilates to form the true stem, which is usually the less digestible component of the plant. Rodriguez and Blanco (1970) reported that the partitioning of dry matter to leaf tissue was greater in a dwarf variety of elephantgrass when compared with 19 tall cultivars. The shape of the contours and response surface (Figs. 20 and 21) indicates that the dry matter production of leaf blades and leaf sheaths in relation to stems was maximized in the region including grazing pressures of about 750 to 1250 kg RLDM ha^{-1} and grazing cycles of 14 to 35 days. It is obvious, in terms of (leaf blade + leaf sheath)/stem ratio and stem growth as already discussed in previous sections, that conditions favorable to stem growth (i.e., low grazing pressures and long grazing cycles) should be avoided in the management of dwarf elephantgrass.

Number of Leaves per Tiller of Dwarf Elephantgrass

The effects of grazing pressure and grazing cycle upon the average number of leaves as well as the average number of senescent and dead leaves per main tiller of dwarf elephantgrass is given in Table 11. The average number of leaves per main tiller varied from 10.4 in pasture 21 (250 kg RLDM ha^{-1} and continuous grazing) to 18.5 in pasture 12 (2500 kg RLDM ha^{-1} and 56-day cycle). The average number of senescent leaves ranged from 0.2 in pasture 24 (250 kg RLDM
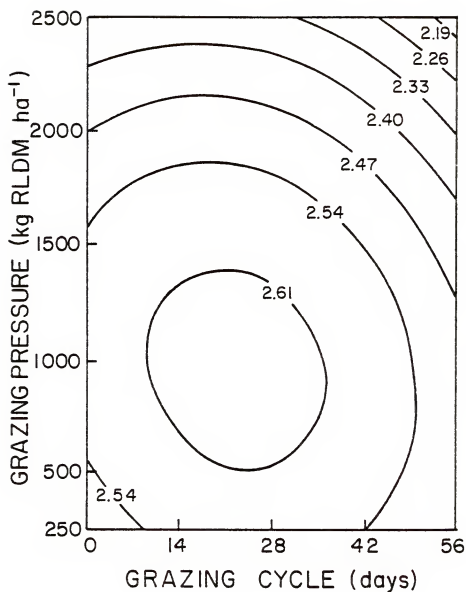
Fig. 20. Contour map of (leaf blade + leaf sheath)/stem
          ratio of dwarf elephantgrass as affected by length
          of grazing cycle and grazing pressure, 1982.
          (R^2 = 0.26, CV = 9.80%)
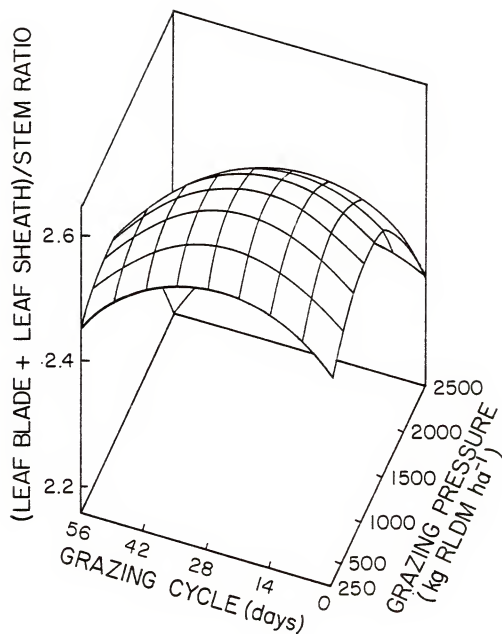
Fig. 21. Response surface of the effect of grazing cycle and
grazing pressure upon (leaf blade + leaf sheath)/stem
ratio of dwarf elephantgrass, 1982. ($R^2 = 0.26$,
CV = 9.80%)

Table 11. Number of leaves of dwarf elephantgrass, before each grazing cycle.

Pasture no.	Estimated grazing pressure	Grazing cycle[†]	Number of leaves per tiller			
			Green	Senescent	Dead	Total
	kg RLDM[‡] ha^{-1}	days				
21	250	cont.[§]	5.8	0.3	4.3	10.4
23	250	cont.	5.7	0.3	5.2	11.2
10	1400	cont.	7.6	0.3	6.3	14.2
26	1400	cont.	7.8	0.3	6.8	14.9
1	2500	cont.	8.2	0.4	7.6	16.0
6	2500	cont.	7.5	0.4	8.2	16.1
9	900	14	6.8	0.3	5.1	12.2
22	900	14	7.0	0.4	5.0	12.4
11	2000	14	8.6	0.3	6.0	14.9
13	2000	14	8.3	0.3	6.8	15.4
4	250	28	6.2	0.6	4.8	11.6
24	250	28	7.5	0.7	6.0	14.2
2	1400	28	7.5	0.7	6.0	14.2
20	1400	28	7.7	0.6	6.7	15.0
7	2500	28	8.3	0.6	9.0	17.9
15	2500	28	7.3	0.5	6.5	14.3
5	900	42	6.8	0.8	7.7	15.3
18	900	42	6.1	0.4	9.3	15.8
16	2000	42	5.5	0.6	10.0	16.1
19	2000	42	7.4	0.6	9.0	17.0
3	250	56	4.6	1.2	5.7	11.5
14	250	56	5.6	0.7	5.5	11.8
8	1400	56	6.4	0.8	10.4	17.6
25	1400	56	6.6	0.5	8.0	15.1
12	2500	56	7.7	0.4	10.4	18.5
17	2500	56	5.0	0.7	9.8	15.5

[†]Grazing cycle = Rest period + 2 days grazing period.
[‡]RLDM = Residual leaf dry matter left after grazing.
[§]Cont. = Continuous grazing.

ha^{-1} and 28-day cycle) to 1.2 in pasture 3 (250 kg RLDM ha^{-1} and 56-day cycle). The number of dead leaves varied from 4.3 in pasture 21 to 10.4 in pasture 12.

The second order model for the number of leaves per tiller accounted for 81% of the total variation. This was divided into 74 and 7% for the linear and quadratic components of the model, respectively (Table 32). For the number of senescent leaves and number of dead leaves the R^2's were 0.52 and 0.76, respectively (Tables 33 and 34). The linear components of the model explained 43 and 70% of the total variation for the number of senescent and dead leaves, respectively. The quadratic and interaction terms accounted for 0 and 9, and 5 and 1% of the variability, respectively.

Independent of the length of grazing cycle, the average number of leaves per tiller is increased when the grazing pressure is decreased (Table 11 and Fig. 22). A greater number of leaves per tiller was observed when low grazing pressures were combined with long grazing cycles. The quadratic effect of grazing pressure, illustrated in Figs. 22 and 23, suggests that frequent and intense defoliations result in the production of a minimum number of leaves per tiller. The lower number of leaves per tiller observed under conditions of higher grazing pressure, even when the grazing cycle is long enough to allow the appearance and extension of new leaves, may be related to a greater elimination of apical meristems in some treatment combinations.

The number of senescent leaves per main tiller was highly variable. Even though Fig. 24 indicates that the number of leaves in

Fig. 22. Contour map of total number of leaves per tiller of
          dwarf elephantgrass as affected by length of grazing
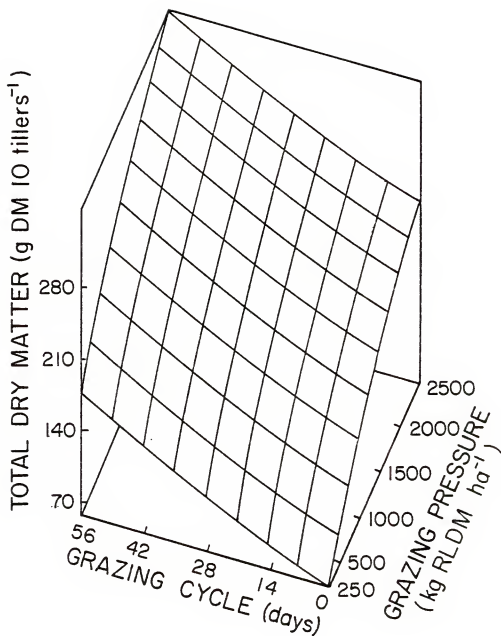   cycle and grazing pressure, 1982. (R^2 = 0.81,
          CV = 7.44%)

Fig. 23. Response surface of the effect of grazing cycle and grazing pressure upon the total number of leaves per tiller of dwarf elephantgrass, 1982. ($R^2 = 0.81$, CV = 7.44%)
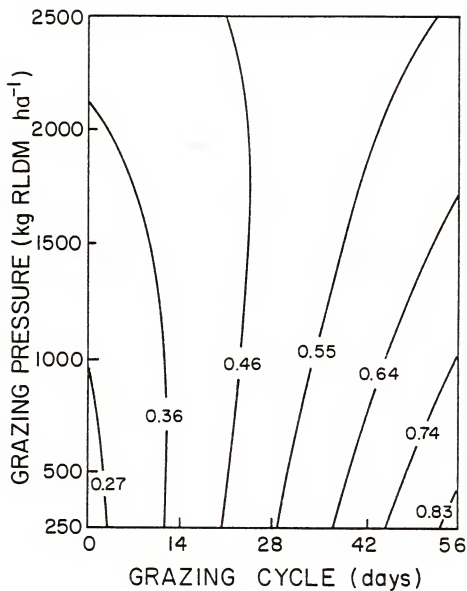
Fig. 24. Contour map of number of senescent leaves per tiller of dwarf elephantgrass as affected by length of grazing cycle and grazing pressure, 1982. (R^2 = 0.52, CV = 34.53%)

senescence was increased as the grazing cycle was increased, the effect of grazing pressure changes from shorter to longer grazing cycles suggesting an interaction of grazing pressure and grazing cycle. Leaf senescence is related to competition for nutrients between old and young leaves as well as to light intensity, length of the day, drought, disease, and mineral nutrition (Laude, 1972; Brady, 1973; Salisbury and Ross, 1978; Wareing and Phillips, 1981). The development of more closed canpies under low grazing pressures, in combination with short and long grazing cycles, may have accelerated the senescence of leaves due to reduced light penetration and increased shading of the tillers (Laude, 1972; Brady, 1973; Wilson and Mannetje, 1978). The greater number of senescent leaves observed under grazing cycles of 56 days and a high grazing pressure (250 kg RLDM ha^{-1}), besides being associated with increased shading, may be due to morphological changes of the plants. These observations are supported by Wilson (1976), Grant et al. (1981), and Wilson and Mannetje (1978) who reported that senescence rate may be affected by reduced light penetration in the sward, higher proportion of more aged tissue, and variation within the tiller due to the effects of leaf position. Furthermore, senescence and death of leaves were more pronounced in the second half of the experimental period and may be associated with a gradual reduction in day length or lack of soil moisture during short periods of time.

An examination of Fig. 25 suggests that the number of dead leaves was increased as the grazing cycle was increased and the grazing pressure was decreased. A quadratic effect of grazing cycle is also

Fig. 25. Contour map of number of dead leaves per tiller of dwarf elephantgrass as affected by length of grazing cycle and grazing pressure, 1982. ($R^2 = 0.76$, CV = 14.54%)

suggested. At lower grazing pressures the increase in the number of
dead leaves was mostly due to an increase in the length of the grazing
cycle. However, the smaller number of dead leaves observed under
higher grazing pressures is not usual and probably is due to a
decrease in the rate of leaf senescence and a reduction in the size
and number of leaves per tiller. Since these measurements were taken
only before each grazing period, there is no doubt that more frequent
recordings are needed in order to establish the rates of appearance
and death of leaves in tillers of dwarf elephantgrass.

Dry Weight of Live and Dead Leaves of Dwarf Elephantgrass

The effect of the experimental variables grazing pressure and
length of grazing cycle upon the dry weight of live and dead leaves
(leaf blades + leaf sheaths), on a 10 tillers basis, is presented in
Table 12. The dry weight of live leaves varied from 25.4 g in pasture
23 (250 kg RLDM ha^{-1} and continuous grazing) to 173.0 g in pasture 12
(2500 kg RLDM ha^{-1} and 56-day cycle). The amount of dead leaves
ranged from 7.0 g in pasture 21 (250 kg RLDM ha^{-1} and continuous
grazing to 102.0 g of dry matter in pasture 17 (2500 kg RLDM ha^{-1} and
56-day cycle).

The dry weight of live leaves was well described by the fitted
model (R^2 = 0.95) (Table 35). The linear component of the model
accounted for 90% of the total variation in this response, while the
quadratic and interaction terms together accounted for about 5%. For
the dry weight of dead leaves the second order model accounted for 81%
of the total variation. Of this 81, 80, 0, and 1% was accounted for

Table 12. Distribution of dry matter in live and dead leaf blades and
           leaf sheaths in tillers of dwarf elephantgrass before each
           grazing cycle.

Pasture no.	Treatment combinations Estimated grazing pressure	Grazing Cycle[†]	Leaf blades + leaf sheaths Live DW[¶]	Dead DW
	kg RLDM ha^{-1}[‡]	days	g DM 10 tillers^{-1}	
21	250	cont.[§]	28.6	7.0
23	250	cont.	25.4	8.2
10	1400	cont.	90.0	32.2
26	1400	cont.	98.4	33.0
1	2500	cont.	109.2	48.8
6	2500	cont.	122.8	58.1
9	900	14	79.2	12.7
22	900	14	88.8	27.3
11	2000	14	114.1	36.4
13	2000	14	107.3	37.5
4	250	28	64.5	13.0
24	250	28	77.2	22.1
2	1400	28	119.4	30.9
20	1400	28	120.9	47.3
7	2500	28	136.2	72.8
15	2500	28	139.0	44.2
5	900	42	106.8	33.8
18	900	42	123.1	41.8
16	2000	42	122.0	69.7
19	2000	42	153.0	68.3
3	250	56	100.0	15.6
14	250	56	101.0	26.0
8	1400	56	154.3	49.4
25	1400	56	152.0	49.5
12	2500	56	173.0	58.0
17	2500	56	157.5	102.0

†Grazing cycle = Rest period + 2 days grazing period.
‡RLDM = Residual leaf dry matter left after grazing.
§Cont. = Continuous grazing.
¶DW = Dry weight.

by the linear, quadratic, and interaction terms, respectively (Table 36).

Dry matter produced by live and dead leaves was increased by reducing the grazing pressure and increasing the grazing cycle (Table 12 and Figs. 26 and 27). The response surfaces of these relationships (Figs. 26 and 27) suggest that the rate of increase in dry matter of live material was progressively increased as grazing cycle was increased and grazing pressure was decreased, whereas the dry matter production of dead material was stimulated under low grazing pressures in combination with long grazing cycles.

It has been indicated that changes affecting forage quality may be related to the rate of leaf development and senescence as well as changes in the composition and digestibility of leaves (Wilson and Mannetje, 1978). At any time, the proportion of live and dead material present in the tillers may affect the quality and intake of the available forage.

For the purpose of grouping the leaf components in live and dead parts, leaves in senescence were considered as dead material. This procedure may have led to an overestimation of dead material in some treatment combinations such as low grazing pressures-long grazing cycles and an underestimation of dead parts in others where senescent leaf blades were eaten due to the imposition of a higher grazing pressure (250 kg RLDM ha-1). Several factors associated with frequency, intensity, and time of defoliation may affect the rate of appearance, senescence, and death of leaves under grazing conditions (Humphreys, 1966, 1981; Jewiss, 1966; Laude, 1972; Brady, 1973; Wilson
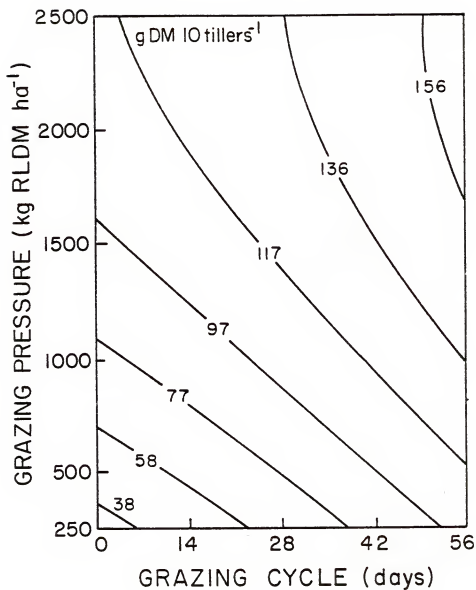
Fig. 26. Contour map of dry matter of live leaf blades +
leaf sheaths of dwarf elephantgrass as affected by
length of grazing cycle and grazing pressure, 1982.
(R^2 = 0.95, CV = 7.86%)
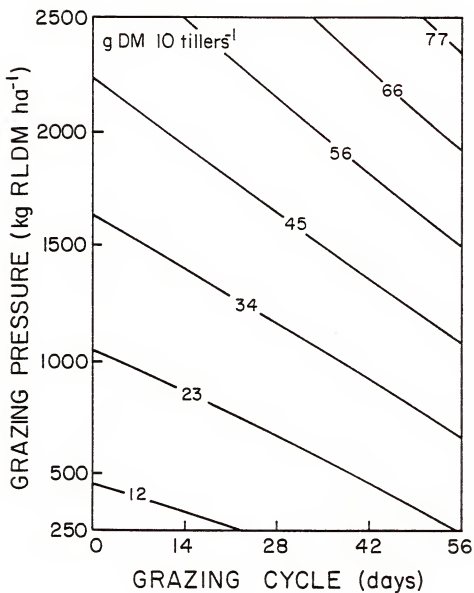
Fig. 27. Contour map of dry matter of dead leaf blades + leaf sheaths of dwarf elephantgrass as affected by length of grazing cycle and grazing pressure, 1982. (R^2 = 0.82, CV = 26.94%)

and Mannetje, 1978; Jones et al., 1982). In some circumstances, the use of higher stocking rates to achieve a desired grazing pressure resulted in the grazing of leaf sheaths, stem apices, and dead leaves in some tillers. A greater proportion of leaves was generally removed at any locus on the main tillers at the beginning of the growing season due to the absence or presence of negligible amounts of dead and senescent leaves. As the growing season progressed, older leaves were defoliated less frequently. In addition to different patterns of removal and their subsequent development, during and after grazing, morphological changes of the plants may have altered the rates of senescence and death of leaves, and hence the dry weight of live and dead leaves in the tillers.

Leaf Area Measurements

These measurements consisted of area of green blades on a 10 tiller basis and of leaf area/leaf weight ratio. The leaf areas are given in cm^2 and the leaf area/leaf weight ratio in cm^2/g DM (Table 13). The leaf area varied from 2003 cm^2 in pasture 23 (250 kg RLDM ha^{-1} and continuous grazing) to 18,876 cm^2 in pasture 12 (2500 kg RLDM ha^{-1} and 56-day cycle). Leaf area/leaf weight ratio ranged from 120.9 cm^2/g DM in pasture 15 (2500 kg RLDM ha^{-1} and 28-day cycle) to 152.1 cm^2/g DM in pasture 21 (250 kg RLDM ha^{-1} and continuous grazing).

The second order model explained 94% of the total variation in leaf area (Table 37). The linear and quadratic components accounted for 91 and 3% of the total variation, respectively (Table 37). For the relationship between leaf area and leaf weight the linear

Table 13. Leaf area and leaf area/leaf weight ratio of dwarf
           elephantgrass tillers, before each grazing cycle.

Pasture no.	Estimated grazing pressure	Grazing Cycle[†]	Leaf area	Leaf area/leaf weight ratio
	kg RLDM ha^{-1}[‡]	days	cm^2 10 tillers^{-1}	cm^2 g^{-1}
21	250	cont.[§]	2245.0	152.1
23	250	cont.	2002.6	148.7
10	1400	cont.	7603.5	135.2
26	1400	cont.	7735.8	129.7
1	2500	cont.	8716.8	119.5
6	2500	cont.	10958.1	132.5
9	900	14	7238.5	136.5
22	900	14	7443.5	126.1
11	2000	14	10712.3	142.1
13	2000	14	10291.1	141.6
4	250	28	5678.4	131.0
24	250	28	6574.3	131.9
2	1400	28	10191.3	129.9
20	1400	28	10875.9	134.4
7	2500	28	11951.6	128.1
15	2500	28	11901.0	120.9
5	900	42	9694.4	130.9
18	900	42	11444.2	132.9
16	2000	42	11801.7	137.6
19	2000	42	14297.5	131.9
3	250	56	8927.7	125.0
14	250	56	8579.2	126.3
8	1400	56	14361.5	126.5
25	1400	56	14447.2	126.0
12	2500	56	18876.0	144.7
17	2500	56	14655.2	122.0

[†]Grazing cycle = Rest period + 2 days grazing period.
[‡]RLDM = Residual leaf dry matter left after grazing.
[§]Cont. = Continuous grazing.

components of the model accounted for 17% of the total variation while the quadratic and interaction terms accounted for 0 and 26%, respectively (Table 38).

An examination of Figs. 28 and 29 indicates that leaf area was increased as the grazing pressure was decreased and the grazing cycle was increased. The quadratic effect of grazing pressure indicates that under continuous grazing and higher grazing pressure the area of green blades was maintained at a minimum (Fig. 29). A lower leaf area per tiller was consistent with the shortening of internodes and reduction in leaf size observed in plants under intensive management and may be interpreted as an adaptive measure or resistance to defoliation (Hodgkinson and Williams, 1983). This observation is also supported by Veiga (1983) who reported that leaf growth rate of this grass is increased as the grazing pressure is reduced and the length of grazing cycle is increased. The growth rate of forage plants is primarily a function of the rate of net photosynthesis and the rate of increase in leaf area. Although photosynthesis occurs in all green surfaces of the plant, i.e., leaf blades, leaf sheaths, stems, and inflorescence, the area of leaf blades is the most useful way to describe the size of the photosynthetic systems (Ludlow, 1976; Whiteman, 1980; Humphreys, 1981). According to Humphreys (1981) the positive relationships between growth and both frequency and intensity of defoliation are due to their effects on the size of the sward canopy. Indeed, the regrowth and dry matter accumulation of tropical grasses have been positively related to residual leaf area index and light interception by the canopy (Ludlow and Charles-Edwards, 1980;
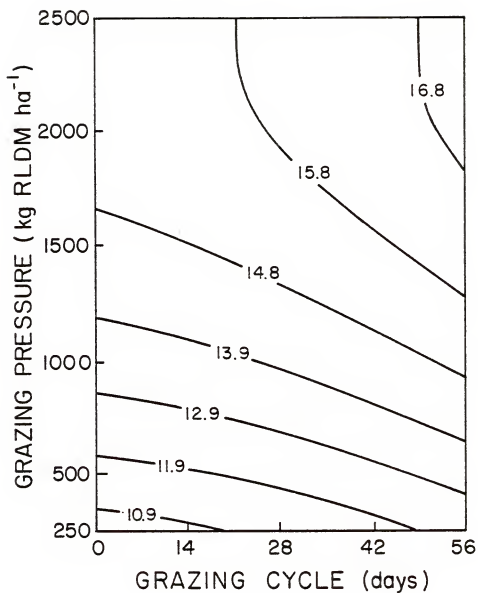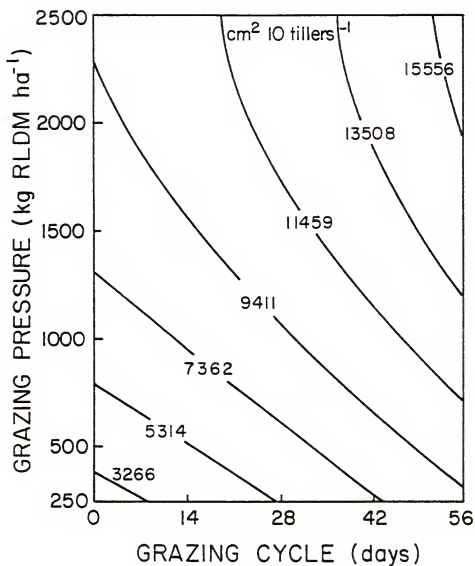
Fig. 28. Contour map of leaf area per 10 tillers of dwarf
elephantgrass as affected by length of grazing cycle
and grazing pressure, 1982. (R^2 = 0.94, CV = 10.27%)
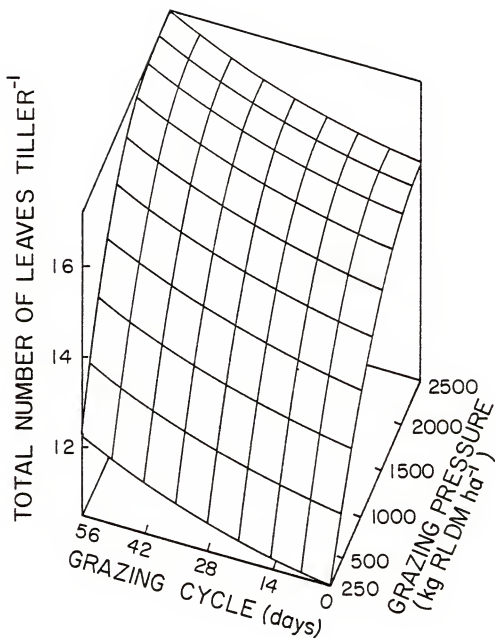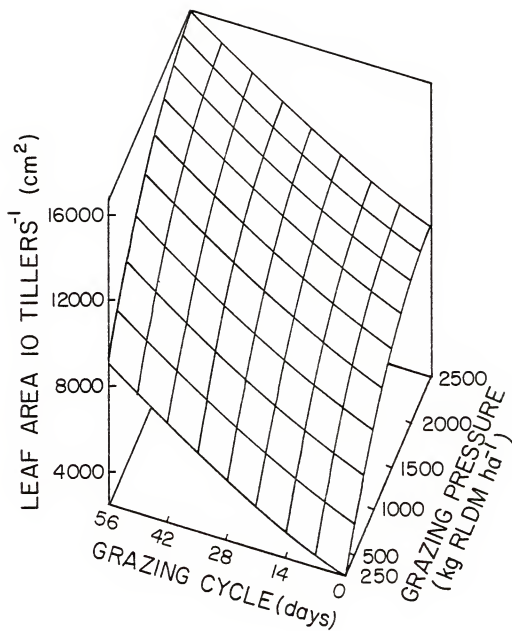
Fig. 29. Response surface of effect of grazing cycle and grazing pressure upon leaf area per 10 tillers of dwarf elephantgrass, 1982. (R^2 = 0.94, CV = 10.27%)

Jones and Carabaly, 1981). In this research, the lower values of leaf area per tiller observed under high grazing pressures and short grazing cycles is related to morphological changes, such as reduction in size of leaves and tillers, and is concomitant with favorable conditions for high leaf area indices at low grazing pressures in combination with long grazing cycles. The leaf area/leaf weight ratios suggest that at higher to medium levels of grazing pressure the leaf area development and the accumulation of dry matter was increased as the grazing cycle was increased (Fig. 30). An interaction of grazing pressure and grazing cycle is also suggested in the response of this relationship which may be associated with the fact that a greater number of older leaves were not grazed at low grazing pressures due to selectivity by the grazing animal.

Total Nonstructural Carbohydrates in Stem Bases of Dwarf Elephantgrass

The average percentages of total nonstructural carbohydrates (TNC) in the stem bases of the grass are given for each pasture in Table 14. The effects of the various treatment combinations on the reserves of the plants were evaluated before and 3 days after each grazing period except for the continuous grazing treatments in which samples taken at 28-day intervals were assumed to reflect the dynamic nature of the continuous treatment. The lowest concentrations of TNC were observed at heavy grazing pressures (250 and 900 kg RLDM ha^{-1}) and short grazing cycles (continuous and 14-day cycles), whereas the highest values were determined at more lenient grazing pressures in combination with long grazing cycles. The TNC concentrations of the
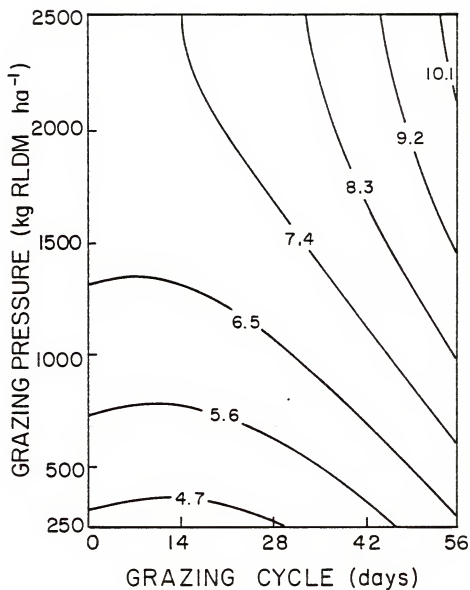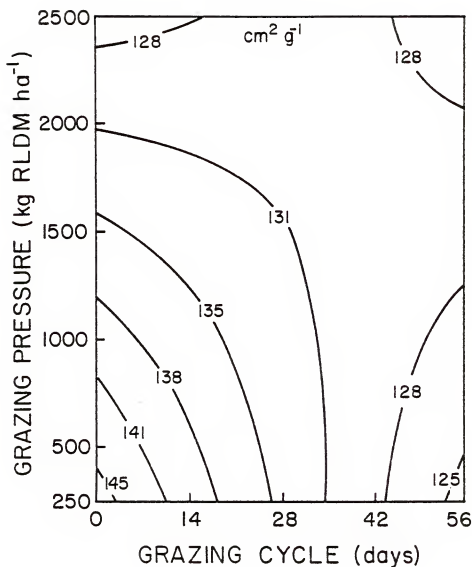
Fig. 30. Contour map of leaf area/leaf weight ratio of dwarf
elephantgrass as affected by length of grazing cycle
and grazing pressure, 1982. ($R^2 = 0.42$, CV = 5.26%)

Table 14. Total nonstructural carbohydrates (TNC) in stem bases of
           dwarf elephantgrass, before and 3 days after each grazing
           period.

Pasture no.	Treatment combinations Estimated grazing pressure	Grazing Cycle[†]	TNC Total nonstructural carbohydrates Before	After
	kg RLDM ha^{-1}[‡]	days	% in DM	
21	250	cont.[§]	8.11	8.11
23	250	cont.	7.68	7.68
10	1400	cont.	9.45	9.45
26	1400	cont.	9.06	9.06
1	2500	cont.	10.28	10.28
6	2500	cont.	10.89	10.89
9	900	14	9.31	7.22
22	900	14	9.20	7.80
11	2000	14	11.15	8.60
13	2000	14	12.73	9.84
4	250	28	11.99	8.73
24	250	28	12.92	10.08
2	1400	28	14.37	12.05
20	1400	28	11.25	9.57
7	2500	28	14.78	10.66
15	2500	28	11.79	8.96
5	900	42	13.87	11.47
18	900	41	13.26	8.25
16	2000	42	13.47	8.07
19	2000	42	14.18	9.68
3	250	56	14.45	9.93
14	250	56	13.57	8.00
8	1400	56	15.68	11.09
25	1400	56	13.82	9.48
12	2500	56	15.19	11.09
17	2500	56	14.16	10.46

[†]Grazing cycle = Rest period + 2 days grazing period.
[‡]RLDM = Residual leaf dry matter left after grazing.
[§]Cont. = Continuous grazing.

stem bases varied from 7.7% in pasture 23 (250 kg RLDM ha^{-1} and continuous grazing) to 15.7% in pasture 8 (2000 kg RLDM ha^{-1} and 56-day cycle).

In samples taken before each grazing period, the second order model for TNC of stem bases accounted for 85% of the total variation. Of this variation, 81, 2, and 2% was accounted for by the linear, quadratic, and interaction terms, respectively (Table 39).

An examination of Table 14 and Figs. 31 and 32 indicates that the variation in TNC concentrations was due mostly to the length of grazing cycle. In general, as the grazing cycle was increased the TNC concentration was increased. However, at short grazing cycles the imposition of more lenient grazing pressures was beneficial to the plants in allowing a fast recovery of reserves. Indeed, under intensive grazing the depletion of reserves may have resulted in a reduction in the number of tillers, plant height, culm height, and length of internodes as well as leaf width as observed by Veiga (1983). Furthermore, lower concentrations of TNC may have contributed to a reduction in the size of the root system of the grass. In plants dug at the end of the experimental period it was observed that larger root systems with well developed rhizomes were present in plants subjected to lower grazing pressures (2000 and 2500 kg RLDM ha^{-1}) and long grazing cycles (42 and 56-day cycles), whereas plants under continuous grazing and high grazing pressures (250 kg RLDM ha^{-1}) had small and thinner root systems in which rhizomes were absent. In addition, the results suggest that, even at higher grazing pressures, a long grazing cycle (28-day cycle) would be sufficient to permit the
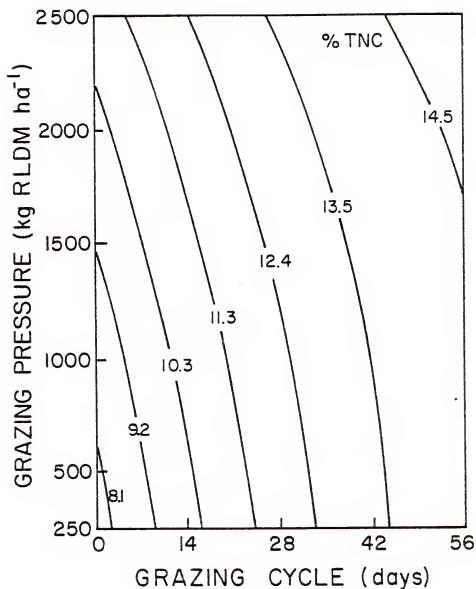
Fig. 31. Contour map of total nonstructural carbohydrates concentration in stem bases of dwarf elephantgrass as affected by length of grazing cycle and grazing pressure, 1982. ($R^2 = 0.86$, CV = 8.11%)
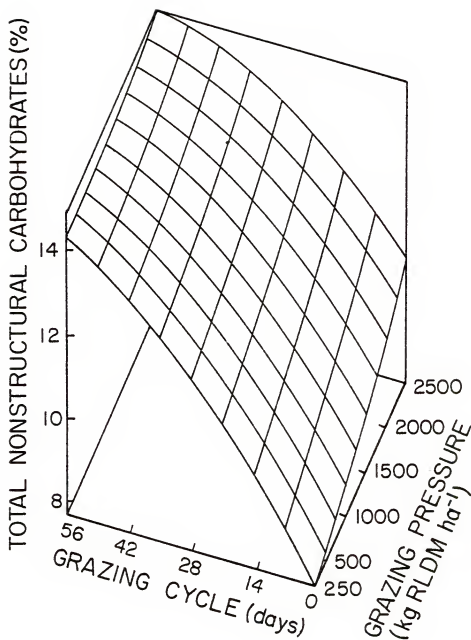
Fig. 32. Response surface of the effect of grazing cycle and grazing pressure upon the total nonstructural carbohydrates in stem bases of dwarf elephantgrass, 1982. ($R^2 = 0.86$, CV = 8.11%)

plants to build up their reserves (Table 14 and Figs. 31 and 32). The maintenance of an adequate level of soluble carbohydrates which could be used by the plants during the initial phase of regrowth or to insure survival after defoliation or periods of climatic stress has been emphasized by several investigators (Humphreys, 1966, 1981; Smith 1972, 1973; Youngner, 1972; White, 1973; Trlica, 1977; Harris, 1978; Deregibus et al., 1982).

Fluctuations of TNC concentrations in stem bases of dwarf elephantgrass followed a similar pattern in all pastures. In general, the level of reserves declined from April to July and increased thereafter towards the end of the growing season. An example of this trend is shown in Fig. 33 for a pasture subjected to high grazing pressures (900 kg RLDM ha^{-1}) and short grazing cycles (14-day cycle). This response is consistent with many reports on reserve carbohydrates of temperate (Brown and Blaser, 1965, 1970; Blaser et al., 1966; Trlica, 1977) and tropical forage species (Wilson and Ford, 1973; Ferraris, 1978; Gomide et al., 1979; Ludlow et al., 1980) in which the use and storage of reserves have been associated with climatic conditions, stage of maturity of the plant, and to frequency, intensity, and time of defoliation.

As was expected, a fall in TNC concentrations was observed 3 days after the end of each defoliation period (Table 14). However, this response is not well accounted for by the second order model (Table 40). The variation in the decline of TNC concentrations may be explained by the sampling procedure adopted as well as by the dynamic nature of the experiment. In some treatment combinations, small
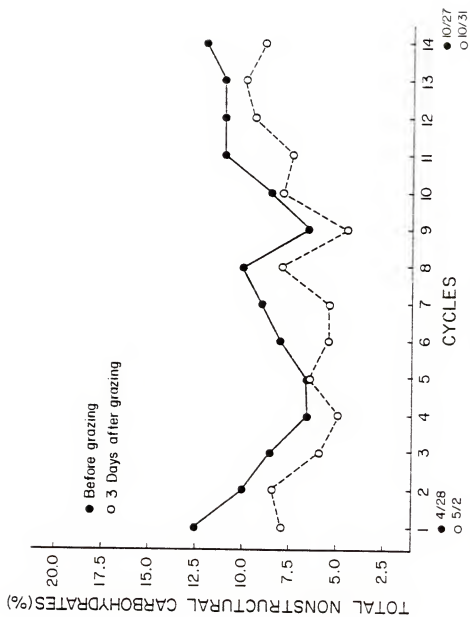
Fig. 33. Total nonstructural carbohydrates in stem bases of dwarf elephantgrass sampled in pasture 9 (14-day grazing cycle and 900 kg RLDM ha^{-1}), 1982.

variations in time to attain a desirable grazing pressure resulted in some samples being collected 4 days after each grazing period instead of 3 days as scheduled.

The reduction of TNC concentrations, even in plants subjected to lower grazing pressures and longer grazing cycles, is supported by several investigations and indicates that reserves were being used to start new growth or at least to maintain the root system alive during the first days after defoliation (Youngner, 1972; White, 1973; Trlica, 1977; Harris, 1978; Deregibus et al., 1982). Similar results with dwarf elephantgrass were obtained by Castillo-Gallegos (1983) in a cutting experiment in which 0, 50, and 100% of leaf area were left after defoliation.

Although regrowth rates in tropical grasses has not been directly associated with TNC concentrations, (Gomide et al., 1979; Jones and Carabaly, 1981; Castillo-Gallegos, 1983), the importance of reserves cannot be ignored.

Larger root systems and higher number of tillers per plant were observed under conditions favorable for build-up of TNC concentrations and maintenance of higher leaf area per tiller; a situation found with more lenient grazing pressures and long grazing cycles. In this context, it is also suggested that short grazing cycles and high grazing pressures should be avoided in the management of dwarf elephantgrass in order to insure the productivity and persistence of the pasture.

SUMMARY AND CONCLUSIONS

A grazing experiment was conducted, from April through November 1982, at the Forage Evaluation Field Laboratory, Beef Research Unit of the University of Florida, Gainesville, to study morphological and physiological responses of dwarf elephantgrass [Pennisetum purpureum (L.) Schum.] under grazing conditions. The soil of the area belongs to Chipley series (Order Entisol), with Pomona series (Order Spodosol) occurring on a small part of the site. The dwarf elephantgrass was propagated vegetatively by both small rooted cuttings and stem cuttings of 5 to 10 cm, planted in 1 m x 1 m spacing. The planting of the grass began in the summer of 1980 and was concluded in July 1981. Irrigation, weed control, and a complete fertilizer with micronutrients were provided during the establishment phase to insure a good stand of plants. In order to test the methodology, a preliminary grazing study was conducted from August to October 1981. Maintenance fertilizer was applied during 1981 and at the beginning of the 1982 grazing season.

Two grazing management factors were studied as experimental variables, a) length of grazing cycle, and b) grazing pressure. The grass was subjected to five levels of each of these variables as follows: length of grazing cycle--continuous grazing, 14, 28, 42, and 56 days and grazing pressure--500, 1000, 1500, 2000, and 2500 kg residual leaf dry matter (RLDM ha^{-1}). Each grazing cycle, except for the continuously grazed treatments, consisted of 2 days of grazing

followed by an appropriate rest period to complete the desired length of grazing cycle.

Response surface methodology was used to study 13 treatment combinations, each with 2 replications, arranged in a modified non-rotatable central composite design. The central treatment (1500 kg RLDM ha^{-1} and 28-day grazing cycle) was selected to represent the region where the combination of experimental variables was anticipated to be near optimum to insure productivity, quality, and persistence of the grass. The data obtained were analyzed using the complete second order polynomial model, $y = b_0 + b_1x_1 + b_2x_2 + b_{11}x_1^2 + b_{22}x_2^2 + b_{12}x_1x_2 + \epsilon$, where y = observed response, x_1 = grazing cycle, and x_2 = estimated grazing pressure.

The size of the experimental pastures was determined by estimating the forage growth rate, the average weight of the grazing animals, the amount of dry matter on offer per 100 kg of body weight per day, the length of the grazing period, and the targeted level of grazing pressure.

Grazing pressure was imposed as residual leaf dry matter in kg ha^{-1} and was estimated by Veiga (1983) using a double sampling technique. Visual estimation was used to determine the level of grazing pressure attained during the grazing period. A variable number of Brown Swiss-Angus crossbred heifers was used to defoliate the pastures according to a previously established schedule. Stocking rates were determined on the basis of available forage, and the number of animals was adjusted during the grazing period in order to achieve the desired grazing pressure in about 2 days.

The response variables obtained before each grazing cycle, consisting of morphological and physiological aspects related to the regrowth of the grass included: plant height, height and percentage of apical meristems eliminated; stem height; number of axillary buds and internodes per tiller; length of internodes; number of main tillers per plant, number of basal, primary, and secondary tillers per tiller; dry weight distribution in leaf blades, leaf sheaths, and stems (measured on 10 tillers); leaf blade/(leaf sheath + stem) ratio and (leaf blade + leaf sheath)/stem ratio; number of leaves per tiller (including total numer of leaves, leaves in senescence, and dead leaves); leaf area and leaf area/leaf weight ratio recorded on 10 tillers, and concentration of total nonstructural carbohydrates (TNC) in the stem bases of the grass.

The results of this research allow the following conclusions:

1. Plant height and stem height increased as the grazing cycle was increased and the grazing pressure was reduced. The apical meristems remained low at high grazing pressures and short grazing cycles and increased in height as the grazing cycle increased and the grazing pressure decreased. The percentage of apical meristems eliminated varied from 25.00 to 73.33% and was greater under continuous grazing and higher grazing pressure. The number of axillary buds per tiller was depressed under high grazing pressures, independent of grazing cycle. The number of internodes per tiller tended to increase as the grazing cycle was increased and the grazing pressure was decreased. The length of internodes was remarkably sensitive to the management imposed. Shorter internodes were observed at short grazing cycles in combination with high grazing pressures.

2. The number of main tillers per plant of dwarf elephantgrass was low and decreased from 34.9 to 15.7 as the grazing cycle was shortened and the grazing pressure was increased. Primary tillers constituted the predominant form of tillering in dwarf elephantgrass under the wide range of management systems studied. The appearance of secondary tilllers was stimulated by high grazing pressure. The number of basal tillers per main tiller increased as the grazing cycle was shortened and the grazing pressure was increased.

※ 3. The DM production in tillers increased by increasing the grazing cycle and reducing the grazing pressure. Dry matter production of leaf blades, leaf sheaths, and stems was higher at long grazing cycles in combination with low grazing pressures.

4. High leaf blade/(leaf sheath + stem) ratios were recorded at long grazing cycles in combination with low and high grazing pressures. The (leaf blade + leaf sheath)/stem ratio values indicated that the DM production of leaf blades and leaf sheaths in relation to stems is at an optimum in the region including grazing cycles of 14 to 35 days and grazing pressures of 750 to 1250 kg RLDM ha⁻1.

5. The average number of leaves per tiller increased when the grazing pressure was decreased, independent of grazing cycle. The number of leaves per tiller was greater when long grazing cycles were combined with low grazing pressures. The number of senescent leaves per main tiller increased as the grazing cycle was increased. Dead leaves per main tiller were increased as the grazing cycle was increased and the grazing pressure decreased.

6. Dry matter produced by live and dead leaves (leaf blades + leaf sheaths) was increased by increasing the length of grazing cycle and by reducing grazing pressure.

7. Leaf area of green leaf blades increased as the grazing cycle increased and the grazing pressure decreased. The leaf area/leaf weight ratios indicated that at high to medium levels of grazing pressure the accumulation of DM is increased as the length of grazing cycle is increased.

8. The TNC concentrations in stem bases were mainly affected by the length of grazing cycle. In general, TNC concentrations increased as the grazing cycle increased. Low concentrations of TNC were observed at short grazing cycles in combination with high grazing pressure. Fluctuations in TNC concentrations followed a similar pattern in all pastures, declining from April to July and increasing thereafter towards the end of the grazing season. After 3 days of regrowth a fall in TNC concentrations was observed in all treatments. It appears that a rest period of about 28 days would be sufficient to permit a build-up of reserves even when the plants were subjected to high grazing pressures.

9. The results obtained indicate that dwarf elephantgrass has the ability to adapt itself to different grazing situations and is a promising species for pastures. The morphological and physiological responses observed indicate that short grazing cycles and high grazing pressures should be avoided in the management of dwarf elephantgrass in order to insure persistence and productivity of the pasture. In this context, after achieving a grazing pressure of 1500 to 2000 kg of RLDM ha^{-1} the animals would be taken out of the pasture which would rest for a period of 28 to 42 days.

APPENDIX

Table 15. Analysis of variance, regression coefficients and probabilities of plant height (cm) of dwarf elephantgrass (x1 = grazing cycle, x2 = grazing pressure), 1982.

RESPONSE MEAN   66.8033
ROOT MSE   3.5038
R-SQUARE   0.97862630
COEF OF VARIATION 0.05237833

REGRESSION	DF	TYPE I SS	R-SQUARE	F-RATIO	PROB
LINEAR	2	10038.3369	0.9435	441.43	0.0001
QUADRATIC	2	105.9341	0.0092	4.31	0.0277
CROSSPRODUCT	1	297.5513	0.0259	24.24	0.0001
TOTAL REGRESS	5	11241.8223	0.9786	163.15	0.0001

RESIDUAL	DF	SS	MEAN SQUARE	F-RATIO	PROB
LACK OF FIT	7	64.5303	9.2186	0.662	0.7002
PURE ERROR	13	180.9960	13.9228		
TOTAL ERROR	20	245.5263	12.2763		

PARAMETER	DF	ESTIMATE	STD DEV	T-RATIO	PROB
INTERCEPT	1	12.0097	2.7143	4.42	0.0003
X1	1	1.2740	0.13068258	9.75	0.0001
X2	1	0.02631207	0.003725510	7.06	0.0001
X1*X1	1	-0.004523858	0.00204624	2.21	0.0387
X1*X2	1	-0.00018799	0.0000381846	-4.92	0.0001
X2*X2	1	.0000018403	.00001259640	-1.46	0.1596

FACTOR	DF	MEAN SQUARE	F-RATIO	PROB
X1	3	6673.3313	2224.4438	181.20	0.0001
X2	3	4825.4856	1608.4952	131.02	0.0001

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Table 16. Analysis of variance, regression coefficients and probabilities of height of apical meristems (cm) of dwarf elephantgrass (x1 = grazing cycle, x2 = grazing pressure), 1982.

RESPONSE MEAN	18.5388
ROOT MSE	1.6988
R-SQUARE	0.9400188
COEFF OF VARIATION	0.09163513

REGRESSION	DF	TYPE I SS	R-SQUARE	F-RATIO	PROB
LINEAR	2	878.4259	0.9130	152.19	0.0001
QUADRATIC	2	15.8188	0.0164	3.74	0.0897
CROSSPRODUCT	1	10.2049	0.0106	3.54	0.0747
TOTAL REGRESS	5	904.4496	0.9400	62.68	0.0001

RESIDUAL	DF	SS	MEAN SQUARE	F-RATIO	PROB
LACK OF FIT	7	7.5119	1.0731	0.278	0.9517
PURE ERROR	13	50.2067	3.8621		
TOTAL ERROR	20	57.7187	2.8859		

PARAMETER	DF	ESTIMATE	STD DEV	T-RATIO	PROB
INTERCEPT	1	5.5751	1.3160	4.24	0.0004
X1	1	0.00916506	0.06736170	0.14	0.8864
X2	1	0.00882454	0.00180616	4.89	0.0001
X1*X1	1	0.002311167	0.00009212	2.33	0.0304
X1*X2	1	-.000348143	.00001951338	-1.38	0.0747
X2*X2	1	-4.15625E-07	6.10740E-07	-0.68	0.5040

FACTOR	DF	SS	MEAN SQUARE	F-RATIO	PROB
X1	3	115.0390	38.3463	13.29	0.0001
X2	3	804.1167	268.0389	92.88	0.0001

Table 17. Analysis of variance, regression coefficients and probabilities of apical meristems elimination (%) of dwarf elephantgrass (x1 = grazing cycle, x2 = grazing pressure), 1982.

RESPONSE MEAN	0.45843061
ROOT MSE	0.05392992
R-SQUARE	0.80982688
COEF OF VARIATION	0.11764032

REGRESSION	DF	TYPE 1 SS	R-SQUARE	F-RATIO	PROB
LINEAR	2	0.18560039	0.6068	31.91	0.0001
QUADRATIC	2	0.06182084	0.2021	10.63	0.0007
CROSSPRODUCT	1	0.00028255	0.0009	0.10	0.7585
TOTAL REGRESS	5	0.24770373	0.8098	17.03	0.0001

RESIDUAL	DF	SS	MEAN SQUARE	F RATIO	PROB
LACK OF FIT	7	0.02249060	0.00321294	1.171	0.3819
PURE ERROR	13	0.03567813	0.00274447		
TOTAL ERROR	20	0.05816873	0.00290844		

PARAMETER	DF	ESTIMATE	STD DEV	T-RATIO	PROB
INTERCEPT	1	0.71788152	0.04177806	17.18	0.0001
X1	1	-0.00100351	0.00201147	-0.50	0.6233
X2	1	-0.00029287	0.0005733813	-5.11	0.0001
X1*X1	1	-0.000405597	0.0000314957	1.29	0.2125
X1*X2	1	-1.831893E-07	5.4773AE-07	0.31	0.7585
X2*X2	1	8.905777E-03	1.93846E-08	4.59	0.0002

FACTOR	DF	SS	MEAN SQUARE	F-RATIO	PROB
X1	3	0.14187759	0.04729253	10.26	0.0001
X2	3	0.11061790	0.03687263	12.68	0.0001

Table 18. Analysis of variance, regression coefficients and probabilities of stem height (cm) of dwarf elephantgrass (x1 = grazing cycle, x2 = grazing pressure), 1982.

RESPONSE MEAN   28.7389
ROOT MSE   1.8431
R-SQUARE   0.95295364
COEF OF VARIATION   0.06413133

REGRESSION	DF	TYPE I SS	R-SQUARE	F-RATIO	PROB
LINEAR	2	1321.6941	0.9152	194.53	0.0001
QUADRATIC	2	19.4109	0.0134	2.86	0.0810
CROSSPRODUCT	1	35.0952	0.0243	10.33	0.0044
TOTAL REGRESS	5	1376.2064	0.9530	81.02	0.0001

RESIDUAL	DF	SS	MEAN SQUARE	F-RATIO	PROB
LACK OF FIT	7	4.3143	0.61632852	0.126	0.9947
PURE ERROR	13	63.6276	4.9544		
TOTAL ERROR	20	67.9419	3.3971		

PARAMETER	DF	ESTIMATE	STD DEV	T-RATIO	PROB
INTERCEPT	1	10.8432	1.4278	7.59	0.0001
X1	1	0.09222763	0.06874445	1.34	0.1948
X2	1	0.01297537	0.00195960	6.57	0.0001
X1*X1	1	0.00218057	0.00107641	2.03	0.0555
X1*X2	1	-.0000645622	.0000203666	-3.21	0.0044
X2*X2	1	-0.0000010181	6.62624E-07	-1.63	0.1184

FACTOR	DF	SS	MEAN SQUARE	F-RATIO	PROB
X1	3	220.2589	73.41966	21.61	0.0001
X2	3	1197.9961	399.3320	117.55	0.0001

Table 19. Analysis of variance, regression coefficients and probabilities of number of axillary buds per tiller of dwarf elephantgrass (x1 = grazing cycle, x2 = grazing pressure), 1982.

RESPONSE MEAN 11.2494
ROOT MSE 1.05935
R-SQUARE 0.8840045
COEFF OF VARIATION 0.09364609

REGRESSION	DF	TYPE I SS	R-SQUARE	F-RATIO	PROB
LINEAR	2	162.1292	0.8438	73.05	0.0001
QUADRATIC	2	3.1377	0.0163	1.41	0.2665
CROSSPRODUCT	1	4.6749	0.0243	4.21	0.0534
TOTAL REGRESS	5	169.9418	0.8845	30.63	0.0001

RESIDUAL	DF	SS	MEAN SQUARE	F-RATIO	PROB
LACK OF FIT	7	6.1552	0.8793085	0.713	0.6633
PURE ERROR	13	16.0404	1.2339		
TOTAL ERROR	20	22.1956	1.1098		

PARAMETER	DF	ESTIMATE	STD DEV	T-RATIO	PROB
INTERCEPT	1	5.2470	0.81609836	6.43	0.0001
X1	1	0.01041556	0.03929184	0.27	0.7917
X2	1	0.00458918	0.00112004	4.10	0.0006
X1*X1	1	0.00095147	0.00061524	1.55	0.1377
X1*X2	1	-0.00025635	0.00011480E-02	-2.05	0.0534
X2*X2	1	-3.593065E-07	3.78732E-07	-0.95	0.3534

FACTOR	DF	MEAN SQUARE	F-RATIO	PROB
X1	3	17.7937	5.9312	5.34	0.0072
X2	3	157.8927	52.6309	47.42	0.0001

Table 20. Analysis of variance, regression coefficients and probabilities of number of internodes per tiller of dwarf elephantgrass (x1 = grazing cycle, x2 = grazing pressure), 1982.

RESPONSE MEAN   15.9772
ROOT MSE   1.0865
R-SQUARE   0.81649700
COEF OF VARIATION   0.06800476

REGRESSION	DF	TYPE I SS	R-SQUARE	F-RATIO	PROB
LINEAR	2	104.1940	0.8098	44.13	0.0001
QUADRATIC	2	0.47790981	0.0037	0.20	0.8184
CROSSPRODUCT	1	0.38408842	0.0030	0.33	0.5749
TOTAL REGRESS	5	105.0559	0.8165	17.80	0.0001

RESIDUAL	DF	SS	MEAN SQUARE	F-RATIO	PROB
LACK OF FIT	7	7.0303	1.0043	0.787	0.6101
PURE ERROR	13	16.5805	1.2754		
TOTAL ERROR	20	23.6107	1.1805		

PARAMETER	DF	ESTIMATE	STD DEV	T-RATIO	PROB
INTERCEPT	1	11.9544	0.84170149	14.20	0.0001
X1	1	0.00036162	0.04052503	0.01	0.9930
X2	1	0.00301357	0.00115519	2.61	0.0168
X1*X1	1	0.00036496	0.00063454	0.58	0.5716
X1*X2	1	-0.000067541	0.00001184115	-0.57	0.5748
X2*X2	1	-1.46207E-07	3.906185E-07	-0.38	0.7084

FACTOR	DF	SS	MEAN SQUARE	F-RATIO	PROB
X1	3	2.1990	0.73300635	0.62	0.6097
X2	3	103.4809	34.4936	29.22	0.0001

Table 21. Analysis of variance, regression coefficients and probabilities of length of internodes (cm) of tillers of dwarf elephantgrass (x1 = grazing cycle, x2 = grazing pressure), 1982.

RESPONSE MEAN	1.1333
ROOT MSE	0.06552955
R-SQUARE	0.9427420
COEF OF VARIATION	0.05782404

REGRESSION	DF	TYPE 1 SS	R-SQUARE	F-RATIO	PROB
LINEAR	2	1.134	0.8028	152.93	0.0001
QUADRATIC	2	0.05065987	0.0341	5.90	0.0097
CROSSPRODUCT	1	0.03780368	0.0254	8.80	0.0076
TOTAL REGRESS	5	1.4019	0.9423	65.29	0.0001

RESIDUAL	DF	SS	MEAN SQUARE	F-RATIO	PROB
LACK OF FIT	7	0.01748188	0.00249741	0.475	0.8364
PURE ERROR	13	0.06840057	0.00526158		
TOTAL ERROR	20	0.08588245	0.00429412		

PARAMETER	DF	ESTIMATE	STD DEV	T-RATIO	PROB
INTERCEPT	1	0.58063907	0.05076398	11.44	0.0001
X1	1	0.00036179	0.00244411	0.15	0.8838
X2	1	0.00039543	0.00006967003	5.68	0.0001
X1*X1	1	0.00012862	0.00003827013	3.36	0.0031
X1*X2	1	-0.000002119	7.14153E-07	-2.97	0.0076
X2*X2	1	-1.18068E-08	2.35586E-08	-1.35	0.1910

FACTOR	DF	SS	MEAN SQUARE	F-RATIO	PROB
X1	3		0.11986635	29.83	0.0001
X2	3	1.1323	0.37742233	87.90	0.0001

Table 22. Analysis of variance, regression coefficients and probabilities of number of main tillers per plant of dwarf elephantgrass (x1 = grazing cycle, x2 = grazing pressure), 1982.

RESPONSE MEAN	25.9512
ROOT MSE	3.7741
R-SQUARE	0.60063601
COEF OF VARIATION	0.14542890

REGRESSION	DF	TYPE 1 SS	R-SQUARE	F-RATIO	PROB
LINEAR	2	360.1376	0.5161	12.92	0.0002
QUADRATIC	2	9.7969	0.0137	0.34	0.7131
CROSSPRODUCT	1	50.5017	0.0708	3.55	0.0743
TOTAL REGRESS	5	428.4363	0.6006	6.02	0.0015

RESIDUAL	DF	SS	MEAN SQUARE	F-RATIO	PROB
LACK OF FIT	7	165.4225	23.7032	2.591	0.0657
PURE ERROR	13	118.9473	9.1498		
TOTAL ERROR	20	284.8698	14.2435		

PARAMETER	DF	ESTIMATE	STD DEV	T-RATIO	PROB
INTERCEPT	1	15.3034	2.9237	5.23	0.0001
X1	1	0.13452966	0.14076409	0.96	0.3506
X2	1	0.00566110	0.00401256	1.41	0.1737
X1*X1	1	0.00181328	0.00220410	0.82	0.4204
X1*X2	1	-.0000774475	.0004113035	-1.88	0.0743
X2*X2	1	-7.89525E-08	.00000135682	-0.06	0.9542

FACTOR	DF	SS	MEAN SQUARE	F-RATIO	PROB
X1	3	240.5351	80.1784	5.63	0.0058
X2	3	239.6533	79.8844	5.61	0.0059

Table 23. Analysis of variance, regression coefficients and probabilities of number of basal tillers per tiller of dwarf elephantgrass (x1 = grazing cycle, x2 = grazing pressure), 1982.

RESPONSE MEAN	0.20924556	
ROOT MSE	0.08212594	
R-SQUARE	0.74088919	
COEF OF VARIATION	0.39248592	

REGRESSION	DF	TYPE I SS	R-SQUARE	F-RATIO	PROB
LINEAR	2	0.32051380	0.6157	23.76	0.0001
QUADRATIC	2	0.05291137	0.1017	3.92	0.0365
CROSSPRODUCT	1	0.01227260	0.0236	1.82	0.1924
TOTAL REGRESS	5	0.38570777	0.7409	11.44	0.0001

RESIDUAL	DF	SS	MEAN SQUARE	F-RATIO	PROB
LACK OF FIT	7	0.07388968	0.01055567	2.249	0.0982
PURE ERROR	13	0.06100371	0.00469259		
TOTAL ERROR	20	0.13489339	0.00674467		

PARAMETER	DF	ESTIMATE	STD DEV	T-RATIO	PROB
INTERCEPT	1	0.56744959	0.06362074	8.92	0.0001
X1	1	-0.00638483	0.00306312	2.08	0.0502
X2	1	-0.00033658	0.00008731605	-3.85	0.0010
X1*X1	1	.00006769151	0.00004796264	1.41	0.1735
X1*X2	1	.00000120732	8.95024E-07	1.35	0.1924
X2*X2	1	6.18981E-08	2.95252E-08	2.10	0.0490

FACTOR	DF	SS	MEAN SQUARE	F-RATIO	PROB
X1	3	0.03484598	0.01161533	1.72	0.1946
X2	3	0.35041293	0.11680431	17.32	0.0001

Table 24. Analysis of variance, regression coefficients and probabilities of number of primary tillers per tiller of dwarf elephantgrass (x1 = grazing cycle, x2 = grazing pressure), 1982.

RESPONSE MEAN	2.7123
ROOT MSE	0.40196517
R-SQUARE	0.37990088
COEF OF VARIATION	0.14820007

REGRESSION	DF	TYPE I SS	R-SQUARE	F-RATIO	PROB
LINEAR	2	0.82893060	0.1590	2.57	0.1019
QUADRATIC	2	0.08490559	0.0163	0.26	0.7716
CROSSPRODUCT	1	1.0667	0.2047	0.60	0.0183
TOTAL REGRESS	5	1.9905	0.3800	2.45	0.0690

RESIDUAL	DF	SS	MEAN SQUARE	F-RATIO	PROB
LACK OF FIT	7	0.68048999	0.09721286	0.495	0.8219
PURE ERROR	13	2.2510	0.19623308		
TOTAL ERROR	20	3.2315	0.16157600		

PARAMETER	DF	ESTIMATE	STD DEV	T-RATIO	PROB
INTERCEPT	1	3.5724	0.31139162	11.47	0.0001
X1	1	-0.01349541	0.01499243	-0.90	0.3788
X2	1	-0.00066443	0.00042737	-1.55	0.1357
X1*X1	1	-0.00014663	0.00023475	-0.62	0.5393
X1*X2	1	.0001125576	.00004380069	2.57	0.0183
X2*X2	1	6.930646E-08	1.44511E-07	0.48	0.6343

FACTOR	DF	SS	MEAN SQUARE	F-RATIO	PROB
X1	3	1.5287	0.50957249	3.15	0.0475
X2	3	1.5389	0.51297627	3.17	0.0465

Table 25. Analysis of variance, regression coefficients and probabilities of number of secondary tillers per tiller of dwarf elephantgrass (x1 = grazing cycle, x2 = grazing pressure), 1982.

RESPONSE MEAN	0.11796600
ROOT MSE	0.10884297
R-SQUARE	0.42419328
COEF OF VARIATION	0.92265769

REGRESSION	DF	TYPE 1 SS	R-SQUARE	F-RATIO	PROB
LINEAR	2	0.09172399	0.2229	3.87	0.0379
QUADRATIC	2	0.08288373	0.2013	3.50	0.0499
CROSSPRODUCT	1	0.00001147277	0.0000	0.00	0.9755
TOTAL REGRESS	5	0.17454919	0.4242	2.95	0.0375

RESIDUAL	DF	SS	MEAN SQUARE	F-RATIO	PROB
LACK OF FIT	7	0.08685156	0.01240737	1.075	0.4312
PURE ERROR	13	0.15008430	0.01154495		
TOTAL ERROR	20	0.23693586	0.01184679		

PARAMETER	DF	ESTIMATE	STD DEV	T-RATIO	PROB
INTERCEPT	1	0.27190677	0.08431773	3.22	0.0042
X1	1	-0.00731600	0.00405961	1.80	0.0866
X2	1	-0.00027532	0.00011572	-2.38	0.0274
X1*X1	1	-0.00013947	0.00006356575	-2.19	0.0402
X1*X2	1	3.69138E-08	0.00001118619	0.03	0.9755
X2*X2	1	7.34207E-08	3.91303E-08	1.88	0.0753

FACTOR	DF	MEAN SQUARE	F-RATIO	PROB
X1	3	0.05919312	1.67	0.2064
X2	3	0.13273347	3.75	0.0275

Table 26. Analysis of variance, regression coefficients and probabilities of total dry matter
(g 10 tillers^{-1}) of dwarf elephantgrass (x1 = grazing cycle, x2 = grazing pressure), 1982.

RESPONSE MEAN	217.3745		
ROOT MSE	19.01132		
R-SQUARE	0.95669674		
COEF OF VARIATION	0.08746765		

REGRESSION	DF	TYPE I SS	R-SQUARE	F-RATIO	PROB
LINEAR	2	157623	0.9441	218.01	0.0001
QUADRATIC	2	2103.6294	0.0126	2.91	0.0778
CROSSPRODUCT	1	6.9650	0.0000	0.02	0.8910
TOTAL REGRESS	5	159733	0.9567	88.37	0.0001

RESIDUAL	DF	SS	MEAN SQUARE	F-RATIO	PROB
LACK OF FIT	7	3165.4333	452.2048	1.446	0.2682
PURE ERROR	13	4064.6332	312.6641		
TOTAL ERROR	20	7230.0665	361.5033		

PARAMETER	DF	ESTIMATE	STD DEV	T-RATIO	PROB
INTERCEPT	1	30.3544	14.7290	2.06	0.0526
X1	1	1.6409	0.70915286	2.31	0.0314
X2	1	0.12411227	0.02021482	6.14	0.0001
X1*X1	1	0.00922856	0.01110399	0.83	0.4157
X1*X2	1	-.000287618	0.00020721	-0.14	0.8910
X2*X2	1	-.000162923	.000000633548	-2.38	0.0272

FACTOR	DF	SS	MEAN SQUARE	F-RATIO	PROB
X1	3	49475.3737	16491.7912	45.62	0.0001
X2	3	110512	36837.3595	101.90	0.0001

Table 27. Analysis of variance, regression coefficients and probabilities of leaf dry matter (g 10 tillers^{-1}) of dwarf elephantgrass (x1 = grazing cycle, x2 = grazing pressure), 1982.

RESPONSE MEAN	97.3206
ROOT MSE	8.4220
R-SQUARE	0.96638520
COEF OF VARIATION	0.08653881

REGRESSION	DF	TYPE I SS	R-SQUARE	F-RATIO	PROB
LINEAR	2	40344.6646	0.9560	284.40	0.0001
QUADRATIC	2	432.7901	0.0103	3.05	0.0698
CROSSPRODUCT	1	5.7297	0.0001	0.08	0.7792
TOTAL REGRESS	5	40783.1924	0.9664	115.00	0.0001

RESIDUAL	DF	SS	MEAN SQUARE	F-RATIO	PROB
LACK OF FIT	7	396.4249	56.9178	0.725	0.6542
PURE ERROR	13	1020.1799	78.4754		
TOTAL ERROR	20	1416.6048	70.9302		

PARAMETER	DF	ESTIMATE	STD DEV	T-RATIO	PROB
INTERCEPT	1	7.0688	6.5243	1.08	0.2915
X1	1	0.71296469	0.31412277	2.27	0.0344
X2	1	0.05518006	0.00895425	6.16	0.0001
X1*X1	1	0.00769967	0.00491857	1.57	0.1332
X1*X2	1	.00002008678	.00009170463	.23	0.7792
X2*X2	1	-.00000066016	.00000302781	-2.18	0.0414

FACTOR	DF	SS	MEAN SQUARE	F-RATIO	PROB
X1	3	15475.0087	5158.3362	72.72	0.0001
X2	3	25436.2730	8478.7577	119.54	0.0001

Table 28. Analysis of variance, regression coefficients and probabilities of leaf sheath dry matter (g 10 tillers^{-1}) of dwarf elephantgrass (x1 = grazing cycle, x2 = grazing pressure), 1982.

RESPONSE MEAN	53.0016
ROOT MSE	6.3238
R-SQUARE	0.87533755
COEF OF VARIATION	0.11931243

REGRESSION	DF	TYPE I SS	R-SQUARE	F-RATIO	PROB
LINEAR	2	5199.8129	0.8105	65.01	0.0001
QUADRATIC	2	356.4856	0.0556	4.46	0.0251
CROSSPRODUCT	1	59.6044	0.0093	1.49	0.2363
TOTAL REGRESS	5	5615.9030	0.8753	28.09	0.0001

RESIDUAL	DF	SS	MEAN SQUARE	F-RATIO	PROB
LACK OF FIT	7	274.1234	39.1605	0.963	0.4920
PURE ERROR	13	525.6734	40.4364		
TOTAL ERROR	20	799.7969	39.9898		

PARAMETER	DF	ESTIMATE	STD DEV	T-RATIO	PROB
INTERCEPT	1	11.2178	4.8988	2.29	0.0330
X1	1	0.50505687	0.23586232	2.12	0.0467
X2	1	0.035543748	0.00672339	5.27	0.0001
X1*X1	1	-0.00129432	0.00369744	-0.35	0.7297
X1*X2	1	-0.000841383	0.00000391744	-1.22	0.2363
X2*X2	1	-0.0000064545	0.00000227346	-2.84	0.0101

FACTOR	DF	MEAN SQUARE	F-RATIO	PROB
X1	3	1121.9254	373.9751	9.35	0.0005
X2	3	4510.8513	1503.6171	37.60	0.0001

Table 29. Analysis of variance, regression coefficients and probabilities of stem dry matter (g 10 tillers^{-1}) of dwarf elephantgrass (x1 = grazing cycle, x2 = grazing pressure), 1982.

RESPONSE MEAN	67.0523
ROOT MSE	7.3519
R-SQUARE	0.93587418
COEF OF VARIATION	0.10964390

REGRESSION	DF	TYPE 1 SS	R-SQUARE	F-RATIO	PROB
LINEAR	2	15678.4508	0.9301	145.04	0.0001
QUADRATIC	2	90.8413	0.0054	0.84	0.4462
CROSSPRODUCT	1	7.2231	0.0004	0.13	0.7185
TOTAL REGRESS	5	15776.5152	0.9359	58.38	0.0001

RESIDUAL	DF	SS	MEAN SQUARE	F-RATIO	PROB
LACK OF FIT	7	591.5083	84.5012	2.244	0.0988
PURE ERROR	13	489.4939	37.6534		
TOTAL ERROR	20	1081.0021	54.0501		

PARAMETER	DF	ESTIMATE	STD DEV	T-RATIO	PROB
INTERCEPT	1	12.0678	5.6553	2.12	0.0468
X1	1	0.42703402	0.27420918	1.56	0.1344
X2	1	0.03349472	0.00781649	4.29	0.0004
X1*X1	1	0.00282321	0.00429359	0.66	0.5183
X1*X2	1	-.00002928969	0.00008012214	0.37	0.7185
X2*X2	1	-.0000032362	0.00000264309	-1.22	0.2350

FACTOR	DF	MEAN SQUARE	F-RATIO	PROB
X1	3	4341.8621	26.78	0.0001
X2	3	11463.3454	70.70	0.0001

Table 30. Analysis of variance, regression coefficients and probabilities of leaf blade/(leaf sheath + stem) ratio of dwarf elephantgrass ($x1$ = grazing cycle, $x2$ = grazing pressure), 1982.

RESPONSE MEAN	0.81375339		
ROOT MSE	0.07304478		
R-SQUARE	0.73063916		
COEF OF VARIATION	0.08976279		

REGRESSION	DF	TYPE I SS	R-SQUARE	F-RATIO	PROB
LINEAR	2	0.25642231	0.6473	24.03	0.0001
QUADRATIC	2	0.00511899	0.0129	0.48	0.6259
CROSSPRODUCT	1	0.02791089	0.0705	5.23	0.0332
TOTAL REGRESS	5	0.28945218	0.7306	10.85	0.0001

RESIDUAL	DF	SS	MEAN SQUARE	F-RATIO	PROB
LACK OF FIT	7	0.03356645	0.00479378	0.852	0.5661
PURE ERROR	13	0.07315434	0.00562726		
TOTAL ERROR	20	0.10671079	0.00533554		

PARAMETER	DF	ESTIMATE	STD DEV	T-RATIO	PROB
INTERCEPT	1	0.50647592	0.05058583	8.95	0.0001
X1	1	0.00723653	0.00272441	2.66	0.0152
X2	1	0.00017031	.00007766099	2.30	0.0326
X1*X1	1	-0.00010724/	.0000426591/	-0.25	0.8041
X1*X2	1	-.00000018207	7.96056E-07	-2.29	0.0332
X2*X2	1	-2.30865E-08	2.62604E-08	-0.88	0.3898

FACTOR	DF	MEAN SQUARE	SS	F-RATIO	PROB
X1	3	0.21275099	0.07091700	13.29	0.0001
X2	3	0.10365660	0.03455220	6.48	0.0031

Table 31. Analysis of variance, regression coefficients and probabilities of (leaf blade + leaf sheath)/stem ratio of dwarf elephantgrass (x_1 = grazing cycle, x_2 = grazing pressure), 1982.

RESPONSE MEAN	2.47508
ROOT MSE	0.24251355
R-SQUARE	0.26016500
COEF OF VARIATION	0.09795165

REGRESSION	DF	TYPE I SS	R-SQUARE	F-RATIO	PROB
LINEAR	2	0.22104987	0.1395	1.89	0.1777
QUADRATIC	2	0.18183514	0.1144	1.55	0.2374
CROSSPRODUCT	1	0.00989878	0.0062	0.17	0.6860
TOTAL REGRESS	5	0.41363379	0.2602	1.41	0.2664

RESIDUAL	DF	SS	MEAN SQUARE	F-RATIO	PROB
LACK OF FIT	7	0.47270201	0.06752806	1.248	0.3461
PURE ERROR	13	0.70355442	0.05411957		
TOTAL ERROR	20	1.17763	0.05881282		

PARAMETER	DF	ESTIMATE	STD DEV	T-RATIO	PROB
INTERCEPT	1	2.44467	0.18786873	13.02	0.0001
X1	1	0.00671064	0.00904523	0.74	0.4662
X2	1	0.00024136	0.00025784	0.94	0.3604
X1*X1	1	-0.00012755	0.00014163	0.90	0.3785
X1*X2	1	-0.0000010843	.00000264296	0.6860	0.6860
X2*X2	1	-1.13771E-07	8.71046E-08	-1.30	0.2067

FACTOR	DF	MEAN SQUARE		F-RATIO	PROB
X1	3	0.03209095		0.56	0.6480
X2	3	0.29479314		1.67	0.2052

Table 32. Analysis of variance, regression coefficients and probabilities of total number of leaves per tiller of dwarf elephantgrass (x1 = grazing cycle, x2 = grazing pressure), 1982.

RESPONSE MEAN 14.4299
ROOT MSE 1.0742
R-SQUARE 0.8138259
COEF OF VARIATION 0.07444575

REGRESSION	DF	TYPE I SS	R-SQUARE	F-RATIO	PROB
LINEAR	2	91.9051	0.7414	39.82	0.0001
QUADRATIC	2	8.9837	0.0725	3.89	0.0373
CROSSPRODUCT	1	0.0004560	0.0000	0.00	0.9850
TOTAL REGRESS	5	100.8692	0.8138	17.48	0.0001

RESIDUAL	DF	SS	MEAN SQUARE	F-RATIO	PROB
LACK OF FIT	7	7.1866	1.0267	0.840	0.5742
PURE ERROR	13	15.8936	1.2226		
TOTAL ERROR	20	23.0802	1.1540		

PARAMETER	DF	ESTIMATE	STD DEV	T-RATIO	PROB
INTERCEPT	1	9.3508	0.83219109	11.24	0.0001
X1	1	0.0351085	0.04006713	0.34	0.7395
X2	1	0.00510147	0.00114214	4.47	0.0002
X1*X1	1	0.0062138	0.00011706736	0.52	0.6850
X1*X2	1	2.22174E-07			
X2*X2	1	-0.000010774	3.862605E-07	-2.79	0.0113

FACTOR	DF	SS	MEAN SQUARE	F-RATIO	PROB
X1	3	11.1332	3.7111	3.22	0.0448
X2	3	90.0074	30.0025	26.00	0.0001

Table 33. Analysis of variance, regression coefficients and probabilities of number of leaves in senescence per tiller of dwarf elephantgrass (x1 = grazing cycle, x2 = grazing pressure), 1982.

RESPONSE MEAN	0.50145284	
ROOT MSE	0.17315683	
R-SQUARE	0.52160695	
COEF OF VARIATION	0.34531031	

REGRESSION	DF	TYPE I SS	R-SQUARE	F-RATIO	PROB
LINEAR	2	0.53008228	0.4292	9.97	0.0017
QUADRATIC	2	0.00361773	0.0029	0.06	0.9416
CROSSPRODUCT	1	0.11234408	0.0896	3.75	0.0672
TOTAL REGRESS	5	0.65404408	0.5217	4.36	0.0076

RESIDUAL	DF	SS	MEAN SQUARE	F-RATIO	PROB
LACK OF FIT	7	0.15981410	0.02283059	0.675	0.6909
PURE ERROR	13	0.43085168	0.03313474		
TOTAL ERROR	20	0.59066579	0.02998329		

PARAMETER	DF	ESTIMATE	STD DEV	T-RATIO	PROB
INTERCEPT	1	0.23430406	0.13419995	1.75	0.0959
X1	1	0.23159231	0.00645838	1.78	0.0901
X2	1	.000118749	0.00018113	0.10	0.9194
X1*X1	1	-.000008673	0.00000113		0.3125
X1*X2	1	-.000000036528	0.000000011871	0.94	0.5672
X2*X2	1	1.95031E-08	6.22519E-08	0.31	0.7573

FACTOR	DF	SS	MEAN SQUARE	F-RATIO	PROB
X1	3	0.63499539	0.21166513	7.06	0.0020
X2	3	0.13062763	0.04360921	1.45	0.2570

Table 34. Analysis of variance, regression coefficients and probabilities of number of dead leaves per tiller of dwarf elephantgrass (x1 = grazing cycle, x2 = grazing pressure), 1982.

RESPONSE MEAN	7.1221	
ROOT MSE	1.0354	
R-SQUARE	0.75903651	
COEF OF VARIATION	0.14537747	

REGRESSION	DF	TYPE I SS	R-SQUARE	F-RATIO	PROB
LINEAR	2	62.1264	0.6956	28.98	0.0001
QUADRATIC	2	4.8189	0.0540	2.25	0.1317
CROSSPRODUCT	1	0.9639180	0.0104	0.96	0.3637
TOTAL REGRESS	5	67.8717	0.7599	12.66	0.0001

RESIDUAL	DF	SS	MEAN SQUARE	F-RATIO	PROB
LACK OF FIT	7	12.2211	1.7459	2.462	0.0763
PURE ERROR	13	9.2196	0.70919632		
TOTAL ERROR	20	21.4406	1.0720		

PARAMETER	DF	ESTIMATE	STD DEV	T-RATIO	PROB
INTERCEPT	1	3.8763	0.80204041	4.83	0.0001
X1	1	-0.02974585	0.03061779	-0.97	0.4512
X2	1	0.00278873	0.00110082	2.46	0.0231
X1*X1	1	0.00048942	0.00012046	1.79	0.0889
X1*X2	1	.000104894	0.00012367	0.93	0.3637
X2*X2	1	-5.45978E-07	3.72235E-07	-1.47	0.1590

FACTOR	DF	SS	MEAN SQUARE	F-RATIO	PROB
X1	3	27.2048	9.0683	8.46	0.0008
X2	3	42.8265	14.2755	13.32	0.0001

Table 35. Analysis of variance, regression coefficients and probabilities of live leaf blades + leaf sheaths (g DM 10 tillers^{-1}) of dwarf elephantgrass (x1 = grazing cycle, x2 = grazing pressure), 1982.

RESPONSE MEAN	110.1281
ROOT MSE	8.6541
R-SQUARE	0.9547068
COEF OF VARIATION	0.07852231

REGRESSION	DF	TYPE I SS	R-SQUARE	F-RATIO	PROB
LINEAR	2	30023.3042	0.9073	200.44	0.0001
QUADRATIC	2	1268.9469	0.0383	8.47	0.0022
CROSS-PRODUCT	1	302.3556	0.0091	4.04	0.0582
TOTAL REGRESS	5	31594.6068	0.9547	84.37	0.0001

RESIDUAL	DF	SS	MEAN SQUARE	F-RATIO	PROB
LACK OF FIT	7	473.0789	67.6970	0.859	0.5611
PURE ERROR	13	1023.9967	78.7690		
TOTAL ERROR	20	1497.0756	74.8938		

PARAMETER	DF	ESTIMATE	STD DEV	T-RATIO	PROB
INTERCEPT	1	14.3841	6.7041	2.15	0.0444
X1	1	1.13284	0.32777098	3.50	0.0023
X2	1	0.07194249	0.00920103	7.82	0.0001
X1*X1	1	0.00374993	0.00505412	0.74	0.4667
X1*X2	1	-0.00018950	.00009631421	-2.01	0.0582
X2*X2	1	-0.00001280	.00000311126	-4.12	0.0005

FACTOR	DF	SS	MEAN SQUARE	F-RATIO	PROB
X1	3	13014.2743	4338.0914	57.92	0.0001
X2	3	18916.4627	6305.4876	84.19	0.0001

Table 36. Analysis of variance, regression coefficients and probabilities of dead leaf blades + leaf sheaths (g DM 10 tillers⁻¹) of dwarf elephantgrass (x1 = grazing cycle, x2 = grazing pressure), 1982.

RESPONSE MEAN   40.1941
ROOT MSE   10.8287
R-SQUARE   0.81501731
COEF OF VARIATION   0.26940902

REGRESSION	DF	TYPE I SS	R-SQUARE	F-RATIO	PROB
LINEAR	2	10166.5441	0.8019	43.35	0.0001
QUADRATIC	2	20.7121	0.0016	0.09	0.9159
CROSSPRODUCT	1	145.4838	0.0115	1.24	0.2785
TOTAL REGRESS	5	10332.7400	0.8150	17.62	0.0001

RESIDUAL	DF	SS	MEAN SQUARE	F-RATIO	PROB
LACK OF FIT	7	552.9266	78.9895	0.573	0.7659
PURE ERROR	13	1792.2727	137.8671		
TOTAL ERROR	20	2345.1993	117.2600		

PARAMETER	DF	ESTIMATE	STD DEV	T-RATIO	PROB
INTERCEPT	1	3.9025	8.3887	0.47	0.6468
X1	1	0.08464089	0.40408580	0.21	0.8361
X2	1	0.01867506	0.01151300	1.62	0.1204
X1*X1	1	0.00205542	0.00063208	0.42	0.6790
X1*X2	1	0.00013145	0.00011801	1.11	0.2785
X2*X2	1	-2.51059E-07	.0000389303	-0.06	0.9492

FACTOR	DF	SS	MEAN SQUARE	F-RATIO	PROB
X1	3	2062.6030	687.5343	5.86	0.0048
X2	3	8420.2868	2806.7623	23.94	0.0001

Table 37. Analysis of variance, regression coefficients and probabilities of leaf area (cm^2 10 tillers^{-1}) of dwarf elephantgrass (x1 = grazing cycle, x2 = grazing pressure), 1982.

RESPONSE MEAN   9969.0514
ROOT MSE   1023.5033
R-SQUARE   0.9434988
COEF OF VARIATION   0.10266807

REGRESSION	DF	TYPE 1 SS	R-SQUARE	F-RATIO	PROB
LINEAR	2	325128596	0.9102	155.18	0.0001
QUADRATIC	2	11137913	0.0312	5.32	0.0141
CROSSPRODUCT	1	54367253	0.0000	0.01	0.9433
TOTAL REGRESS	5	336271945	0.9413	64.20	0.0001

RESIDUAL	DF	SS	MEAN SQUARE	F-RATIO	PROB
LACK OF FIT	7	4020332	574333	0.441	0.8593
PURE ERROR	13	16930846	1302373		
TOTAL ERROR	20	20951178	1047559		

PARAMETER	DF	ESTIMATE	STD DEV	T-RATIO	PROB
INTERCEPT	1	1061.4110	792.8805	1.34	0.1957
X1	1	85.0663	38.1745	2.23	0.0375
X2	1	6.3865	1.0882	5.87	0.0001
X1*X1	1	0.5725574	0.5971593	0.96	0.3495
X1*X2	1	0.00080557	0.01115933	0.07	0.9433
X2*X2	1	-0.00130796	0.00036796	-3.24	0.0041

FACTOR	DF	MEAN SQUARE	F-RATIO	PROB
X1	3	154456207	49.15	0.0001
X2	3	182767908	58.16	0.0001

Table 38. Analysis of variance, regression coefficients and probabilities of leaf area/leaf weight ratio of dwarf elephantgrass (x1 = grazing cycle, x2 = grazing pressure), 1982.

RESPONSE MEAN	132.4635
ROOT MSE	6.9631
R-SQUARE	0.424430
COEF OF VARIATION	0.05256596

REGRESSION	DF	TYPE I SS	R-SQUARE	F-RATIO	PROB
LINEAR	2	282.4031	0.1675	2.91	0.0776
QUADRATIC	2	2.4706	0.0015	0.03	0.9749
CROSSPRODUCT	1	431.1018	0.2557	8.89	0.0074
TOTAL REGRESS	5	715.9755	0.4247	2.95	0.0372

RESIDUAL	DF	SS	MEAN SQUARE	F-RATIO	PROB
LACK OF FIT	7	497.7155	71.1022	1.958	0.1401
PURE ERROR	13	471.9713	36.3055		
TOTAL ERROR	20	969.6868	48.4843		

PARAMETER	DF	ESTIMATE	STD DEV	T-RATIO	PROB
INTERCEPT	1	148.2171	5.3941	27.48	0.0001
X1	1	-0.50287090	0.25970748	-1.94	0.0671
X2	1	-0.00805044	0.00740312	-1.09	0.2898
X1*X1	1	0.00021661	0.00040663	0.53	0.6239
X1*X2	1	0.00092628	0.00075094	2.20	0.0394
X2*X2	1	-1.40344E-07	0.0000025033	-0.06	0.9553

FACTOR	DF	SS	MEAN SQUARE	F-RATIO	PROB
X1	3	637.6693	212.5564	4.38	0.0159
X2	3	509.0895	169.6965	3.50	0.0345

Table 39. Analysis of variance, regression coefficients and probabilities of total nonstructural carbohydrates (%) in stem bases of dwarf elephantgrass, before grazing (x_1 = grazing cycle, x_2 = grazing pressure), 1982.

RESPONSE MEAN	12.1781
ROOT MSE	0.98773676
R-SQUARE	0.85592456
COEF OF VARIATION	0.08110772

REGRESSION	DF	TYPE I SS	R-SQUARE	F-RATIO	PROB
LINEAR	2	109.7977	0.8107	56.27	0.0001
QUADRATIC	2	2.9715	0.0219	1.52	0.2423
CROSSPRODUCT	1	3.1506	0.0233	3.23	0.0874
TOTAL REGRESS	5	115.9199	0.8559	23.76	0.0001

RESIDUAL	DF	SS	MEAN SQUARE	F-RATIO	PROB
LACK OF FIT	7	4.9900	0.71296119	0.638	0.7178
PURE ERROR	13	14.5224	1.1171		
TOTAL ERROR	20	19.5125	0.97562391		

PARAMETER	DF	ESTIMATE	STD DEV	T-RATIO	PROB
INTERCEPT	1	7.5143	0.76612859	9.81	0.0001
X1	1	0.17925702	0.03607590	4.86	0.0001
X2	1	0.00093430	0.00104512	0.89	0.3820
X1*X1	1	-0.00100719	0.00057717	-1.75	0.0963
X1*X2	1	-0.00001929	0.00001073	-1.80	0.0874
X2*X2	1	1.14041E-07	3.53219E-07	0.32	0.7495

FACTOR	DF	SS	MEAN SQUARE	F-RATIO	PROB
X1	3	106.9022	35.6341	36.52	0.0001
X2	3	12.15519	4.05506	4.15	0.0193

Table 40. Analysis of variance, regression coefficients and probabilities of total nonstructural carbohydrates (%) in stem bases of dwarf elephantgrass, after grazing ($x1$ = grazing cycle, $x2$ = grazing pressure), 1982.

RESPONSE MEAN   9.4959
ROOT MSE   1.7392
R-SQUARE   0.29229989
COEF OF VARIATION   0.13049837

REGRESSION	DF	TYPE I SS	R-SQUARE	F-RATIO	PROB
LINEAR	2	11.7549	0.2709	3.83	0.0391
QUADRATIC	2	0.12387732	0.0029	0.04	0.9605
CROSSPRODUCT	1	0.80635012	0.0186	0.53	0.4771
TOTAL REGRESS	5	12.6852	0.2923	1.65	0.1923

RESIDUAL	DF	SS	MEAN SQUARE	F-RATIO	PROB
LACK OF FIT	7	13.7908	1.9701	1.514	0.2461
PURE ERROR	13	16.9219	1.3017		
TOTAL ERROR	20	30.7126	1.5356		

PARAMETER	DF	ESTIMATE	STD DEV	T-RATIO	PROB
INTERCEPT	1	7.7344	0.96117817	8.05	0.0001
X1	1	0.02032000	0.04626418	0.44	0.6650
X2	1	0.00093073	0.00133120	0.70	0.7679
X1*X1	1	0.00097588	0.00342411	0.27	0.4771
X1*X2	1	-0.00013671	0.000136716	-0.72	0.9813
X2*X2	1	1.05075E-08	4.41091E-07	0.02	

FACTOR	DF	SS	MEAN SQUARE	F-RATIO	PROB
X1	3	4.3594	1.4531	0.95	0.4370
X2	3	9.1455	3.0485	1.99	0.1497

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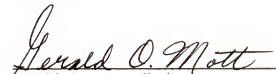
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I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

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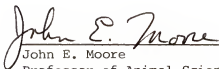
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